MECHANISMS IN CORTEX AND MIDBRAIN CONCERNED WITH EYE MOVEMENTS

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INTRODUCTION

The projection of the retina on the superior colliculus was worked out anatomically on rabbit (Brouwer and Zeeman 1923), rat (Lashley 1934), opossum (Bodian 1937) and the ferret (Jefferson 1940). Lesions were made in the retina and followed by the Marchi method. Recently and for the first time Apter used the electrical method by applying surface electrodes on the surface of the colliculus of cat and shining light in the different parts of the visual field as a stimulus (Apter 1945).

If the projection of the retina on the superior colliculus is to be studied in terms of point to point representation the Marchi technique is quite inadequate because the lesions which were made in the retina were quite large and the results showed the projection of different quadrants of the retina on the superior colliculus in a gross anatomical picture. Moreover in animals as the monkey and cat this method did not give conclusive results, probably due to the small size of the superior colliculus and the crudeness of the Marchi method. The electrical method used by Apter is a great improvement no doubt, but the surface electrodes again are big and it is only the surface of the colliculus that was explored.

In this work I aimed at using microneedle electrodes, and fixing the animal in the stereotaxic instrument and by manipulating the needle I could reach any part of the superior colliculus and thus

have the opportunity to record from the surface, and more important to explore the depths of this structure. The animals used were the rabbit, goat and pigeon.

THE STRUCTURE OF THE SUPERIOR COLLICULUS IN MAMMALS

The structure of the superior colliculus has been studied in many mammals as rat, rabbit, cat, opossum and ferret. (Cajal 1911, Tsai 1925, Tsang 1937, Bodian 1937, Jefferson 1940).

Following the nomenclature of Tsang, the superior colliculus can be divided into six layers:

Layer I Stratum zonale

This is a very thin layer, consisting of small marginal cells, and fine myelinated fibres. It is difficult to demonstrate especially if silver impregnation methods are used. Ganser (1887) denied its existence.

Layer II Stratum griseum superficiale

This is a thick layer, easily demonstrated in toluidin blue stained material, composed of rather small cells.

Layer III Stratum opticum

Also thick and easily shown in sections stained with silver or hematoxylin (Weil). As will be seen later, it is composed of two components, a superficial one, which is the continuation of the fibres of the mesencephalic root of the optic tract and a deeper, which arises from the occipital cortex. There are medium sized cells scattered among the fibres.

Layer IV Stratum lemnisci

The fibres in this layer belong to the lemniscal system and to the brachium of the superior colliculus. Small cells and some giant cells are seen also.

Layer V Stratum album profundum

The cells are small and the fibres are the efferents coming from the superficial layers.

Layer VI Stratum griseum centrale

This is the grey matter surrounding the aqueduct of Sylvius.

Much work has been done to determine which of the above mentioned layers receive optic fibres.

Cajal (1911) came to the conclusion that optic fibres coming from the optic tract partially terminate in the superficial part of the stratum opticum, and partially in the whole thickness of the stratum griseum superficiale. The former he called "arborisations inferieures" and the latter "arborisations superieures". Cajal also says that the terminations in the stratum griseum superficiale are complex, because one optic fibre would make connections with many cells.

As regards the deeper layers and the stratum zonale, Cajal was of the opinion that no optic fibres reach them.

These studies of Cajal were made on the mouse;

after enucleation of one eye, he followed the degeneration in Marchi sections.

Tsang (1937) with an entirely different method tried to determine the sites of termination of optic fibres in the superior colliculus. His work is very good except that he considered the stratum zonale and stratum griseum superficiale as one layer. So, whereas he could easily determine that optic fibres terminate in the stratum griseum superficiale and stratum opticum, he completely ignored the individuality of the stratum zonale. From the description of the method he used, one can be sure that his method cannot answer whether optic fibres end in the stratum zonale or not.

Tsang prepared Weigert sections from normal colliculi and compared them with sections from mice which have been blinded in one eye at infancy using a screw micrometer to measure the depth of the various layers.

The anteroposterior length of the superior colliculus was found to diminish to 76% of the normal control. The cells in the stratum griseum showed atrophy three months after the enucleation of the eye and this atrophy became very pronounced seven to seventeen months after the operation.

In animals killed seven months after the operation, the depth of the stratum zonale plus the stratum griseum superficiale was 18 to 18% of the total depth of the colliculus (control 19%) similarly the depth of the stratum opticum was 80 to 82% of the total (control 86%). The upper part of the stratum opticum which comes from the optic tract vanished completely, whereas the deeper part which comes from the cortex was intact.

All these changes observed by Tsang were in the contralateral colliculus. He found no changes in the ipsilateral one.

Tsai (1925) used normal Weigert preparations and found that fibres of the mesencephalic root of the optic tract ended in the stratum opticum, but when he used silver methods of staining he could follow the fibres to the stratum griseum superficiale also.

Other workers confirmed the results of Cajal by using the Marchi method after enucleation of one eye. Among these we may mention Loepp (1912) Brouwer et al (1923) Overbusch (1927) and Bodian (1937). They all agree that optic fibres end in stratum opticum and stratum griseum superficiale, and none of them could follow fibres to stratum zonale. Jefferson (1940) working on the opossum and using the Marchi method arrived at the same conclusion.

In the available literature we find that two workers do not wholly agree that optic fibres reach the stratum zonale.

Bodian (1937) working on the opossum, studied degenerated material using the Marchi method. He found that retinal fibres from the temporal part of the retina do reach the ipsilateral colliculus in its anterior half and end in the stratum zonale. He also claims that he could follow fibres to the contralateral colliculus, ending in the same stratum but much less in number than those to the ipsilateral one.

More recently Le Gros Clark (cited by Jefferson 1940) cut the optic nerve in four rats. The animals were allowed to live one, two, three and four days respectively after the section, and then killed. Sections in the brain were stained with silver (modified Ranson method). Degeneration granules were well demonstrated in animals killed three or four days after the section (probably had enough time to show the degeneration). The granules represented the degenerated terminals of optic fibres, and could be seen in the stratum opticum, stratum griseum superficiale and the stratum zonale. All were to be found in the contralateral colliculus only. The work of Clark puts it beyond doubt that all the three layers receive optic fibres. Probably he succeeded

where the other workers failed because the terminals reaching the stratum zonale have lost their myelin sheaths before they arrived there and can only be demonstrated with this method, whereas Marchi's technique failed to do so.

The composite origin of the stratum opticum was referred to above.

Cajal (1911) removing one eye in the cat and following the degeneration by the Marchi method, found that it is only the superficial part of the stratum opticum that suffered, whereas the deeper component remained intact and he concluded that this deeper part is composed of fibres coming from the cortex and gave it the name (voie cortico-bigeminale). He followed the fibres in this deeper part and found them to end partly in the stratum opticum itself and partly in the deeper stratum lemnisci which this author had called zone ganglionaire.

Tsang's (1937) work referred to above had also shown that after enucleating one eye the deeper part of the stratum opticum remained intact even after seventeen months survival (before killing the animal).

Then it would be expected that this component would degenerate if its origin in the cortex was damaged. So Barris et al (1935) made lesions

in the striate and peristriate cortex of the cat, they followed the degeneration by Marchi method and could find the granules in the deeper part of the stratum opticum of the ipsilateral colliculus.

Jefferson (1940) got the same results, working on the ferret, but does not agree with Cajal as regards the final destination of these fibres. Cajal, as mentioned above, followed the terminals in the stratum opticum itself and also the stratum lemnisci, but Jefferson suggests that they end in the stratum opticum and the stratum griseum superficiale. In the literature available we could not find any other work that confirms either view.

Although both Barris and Jefferson made these lesions in the occipital lobe, this does not preclude there being other fibres taking origin elsewhere in the cortex as the frontal lobe. This will be referred to later.

It seems that in lower mammals as the rat and rabbit where there is almost complete crossing at the chiasma, no retinal fibres can be demonstrated in the ipsilateral colliculus (Pavlow 1900, Berl 1920, Brouwer et al 1923, Overbosch 1927 and Lashley 1934). This is not the case in higher mammals as primates where uncrossed fibres to the colliculus could be demonstrated as Bodian (1937) had demonstrated in the opossum. These fibres as Bodian describes occupy the most superficial layer

of the stratum opticum and from there they climb up to end in the stratum zonale as mentioned earlier. Bodian went even further and mapped these retinal fibres on the superior colliculus of the opossum. He found that fibres from the upper uncrossed temporal field pass to the anterior and lateral part of the ipsilateral colliculus and fibres from the lower uncrossed temporal field pass to the anterior and medial part of the ipsilateral colliculus and fibres from the intermediate part of the uncrossed temporal field pass to an intermediate area in the anterior part of the ipsilateral superior colliculus.

Recently Apter (1945) working on the cat and using surface electrodes on the colliculus and shining light in front of the eye as a stimulus could map the uncrossed temporal retinal fibres on the colliculus in the same way.

• The opossum is a marsupial and not a primate. The crossing of optic nerve fibres is related to the visual field and not to evolutionary level. As in the cat, the opossum's eyes look straight ahead.

THE STRUCTURE OF THE OPTIC TECTUM IN BIRDS

The optic tectum of birds has quite a different structure from that of mammals. The size is relatively big, and the two structures do not meet each other in the midline, because they are displaced ventrolaterally.

There has been a difference of opinion about the number of layers in the optic tectum of birds. Bellonci (1888) described seven layers, Ramon (1898), Ramon y Cajal (1891) and (1911) fifteen layers, Van Gehuchten (1892) three layers, Von Kolliker (1896) using Weigert material and Ris (1899) using Golgi method nine layers.

Jungherr (1945) studied the mesencephalon in the chicken. He gave a detailed description of the layers of the optic tectum, and ascribed the enormous number of layers to a subdifferentiation of "stratum griseum et fibrosum superficiale". In this description he follows the fundamental pattern of six layers in reptiles and birds, as laid down by Huber and Crosby (1929), which has been amplified due to a subdifferentiation of "stratum griseum et fibrosum superficiale".

The layers as described by Jungherr are listed in order from the surface to the ventricle:

I Stratum zonale

Poorly developed and not present in all reptiles.

II Stratum opticum

Formed by the incoming optic fibres, and delimited centrally by a thin but distinct band of small pale-staining neurons.

III Stratum griseum et fibrosum superficiale

From the surface inwards the following secondary layers can be differentiated:

(a) a cell-poor area underlying stratum opticum,

(b) a broad band of pale-staining small neurons,

(c) a cell-poor area in which fibre fascicles run,

(d) a band of cells consisting of a row of linearly arranged, pale-staining neurons, a narrow, cell-poor fibre area and then a deeply situated line of linearly arranged deeply staining cells, so compactly arranged that their cell bodies cannot always be recognized. Internal to this band, two others may still be differentiated,

(e) a broad band of small scattered neurons,

(f) a layer containing more closely arranged cell bodies,

(g) a broad cell-free zone.

IV Stratum griseum centrale

Consists of a broad, somewhat irregularly delimited band of widely spaced medium sized neurons. These neurons are major contributors to the efferent tectal system.

V Stratum album centrale

A fibre area underlying stratum griseum centrale. Through this white layer the main efferent pathways of the optic tectum run.

VI Stratum griseum periventriculare

Finds representation in the small-celled gray intercalated close to the optic ventricle. Its neurons are so arranged that the dendrites spread toward the ventricle and the neuraxes either enter the efferent layer of stratum album centrale or pass toward the periphery of the tectum.

VII Stratum fibrosum periventriculare

Consists of fibres which circumscribe the ventricle. Into it come fascicles from the hypothalamus, the inferior colliculus and the cerebellum and perhaps from other brain levels.

The nucleus mesencephalicus lateralis pars dorsalis is considered to be the homologue of the mammalian inferior colliculus (Huber and Crosby 1929). It is formed of medium sized pale-staining neurons forming a considerable mass along the ventral aspect of the optic ventricle, from which it is separated by the periventricular gray and fibrous tectal strata. The pretectal nucleus is to be found in the dorsolateral aspect of the diencephalon near its caudal end, (Huber and Crosby 1929).

It seems that stratum griseum et fibrosum superficiale is the site of termination of optic fibres.

To the best of my knowledge the mapping of the retina on the optic tectum of birds has not been done either anatomically or by physiological means.

AFFERENT PATHWAYS TO THE SUPERIOR COLLICULUS

I The mesencephalic root of the optic tract

This has been referred to above as terminating in the superficial layers of the stratum opticum. The majority of the optic tract fibres end in the lateral geniculate body, but a bundle situated on the medial side of the tract passes through the superior quadrigeminal brachium and enters the superior colliculus. (von Monakow 1905)

II Cortico mesencephalic fibres

These have also been referred to as ending in the deeper layers of the stratum opticum.

(a) Frontomesencephalic fibres

These descend in the medial part of the cerebral peduncle and entering the tegmental region of the midbrain, terminate in connection with the superior colliculus or directly with the oculomotor nuclei.

Crosby, Yoss and Henderson (1952) found that in the monkey these fibres go directly to the oculomotor nuclei without relaying in the superior colliculus. They stimulated different parts of the eye field in the frontal cortex in monkey under ether anaesthesia. The animal must be on the verge of consciousness to obtain upward eye movements from the stimulation of the appropriate portion of the frontal cortex.

Downward movements also may be obtained only when the anaesthesia is very light, but horizontal deviations appear when the animal is somewhat more deeply anaesthetised although still under light anaesthesia.

Sherrington (1893) pointed out that the frontal cortex may exert an inhibitory as well as an excitatory effect over the turning of the eyes in various directions.

(b) Occipitomesencephalic fibres

These arise in the occipital lobe and in Weigert stained sections can be seen penetrating the base of the pulvinar and entering the deeper layers of the stratum opticum of the superior colliculus. There is much dispute about the origin of these fibres, whether they arise from the visual area proper, i.e. area 17 or from the peristriate areas 18 and 19.

Polisk (1932) working on monkeys came to the conclusion that they are derived from the peristriate cortex. The same conclusion was arrived at by Foerster (1931). He stimulated the striate area in patients during intracranial operations, but could not elicit any ocular movements, while stimulation of the peristriate areas readily produced the movements.

On the other hand Walker and Weaver (1940) could obtain lateral conjugate deviation of the eyes in monkeys by stimulation of the cortex of the area striata itself. These workers claim even that they obtained a localization in this area. Stimulation of the cortex above the calcarine fissure made the eyes move laterally and downwards and stimulation below this fissure made the eyes move laterally and upwards.

No definite conclusion can be arrived at with this controversy, but whether the cortico-mesencephalic fibres arise from the area striata itself or from the peristriate area, we should not forget the existence of association fibres between these visual areas.

According to the experiments with the strychnine method of Von Bonin, Garol and McCulloch (1942), area 18 has efferent association connections with areas 17 and 19 and also with the opposite area 18 (Monkeys and chimpanzees). This even has to be accepted with caution because of the technique of McCulloch and his co-workers is open to much criticism (Ralph Druckman 1952).

Not all these corticomesencephalic fibres

end in the superior colliculus. There is evidence that some of them do not relay in this structure at all, but go direct to other parts of the midbrain.

Bernheimer (1899) destroyed the superior colliculus and then stimulated the occipital lobe and still obtained eye movements.

More recently Mettler (1935) found that corticomesencephalic fibres in the monkey extend from the upper lip of the calcarine fissure to the oculomotor nucleus, trochlear nucleus, the central grey matter of the aqueduct and fasciculus longitudinalis medialis. Not only this but we must remember that some of these corticomesencephalic fibres are concerned with the light reflex and although they may be with the same bundle in part of their course, yet they have their own destination. Clark (1932) traced fibres from the cortex of the rat to the pretectal nucleus, and Barris (1936) confirmed this fact by stimulation of this cortical area in the cat and got constriction of the pupils.

III Acoustic fibres

These appear to reach the superior colliculus directly from the inferior colliculus (Woollard and Harpman 1940).

IV Fibres reach the superior colliculus from the medial lemniscus either as terminals or as collaterals.
V Fibres from the substantia nigra and possibly other parts of the basal ganglia reach the superior colliculus.

These are some of the afferent pathways reaching the superior colliculus. The importance of each varies in different animals for example in man and primates it is stated that the optic and cortical fibres are the most important.

EFFERENT PATHWAYS FROM THE SUPERIOR COLLICULUS

I Efferent fibres to the nuclei of the oculomotor, trochlear and abducent nerves.

II The tectospinal tract

Arises from the deep cell layers of the superior colliculus. Most of its fibres cross the midline in front of the aqueduct and descend in pons and medulla oblongata immediately anterior to the medial longitudinal fasciculus. It can be followed in the cervical region of the spinal cord where it lies in the ventral column close to the ventral median fissure. It gives collaterals to cranial nerve nuclei in the pons and medulla.

THE RELATION OF THE SUPERIOR COLLICULUS TO THE PATHWAY OF THE LIGHT REFLEX

It was long believed that fibres concerned with constriction of the pupil in response to light traverse the superior colliculus on their way to the oculomotor nucleus. Later it was found that in the monkey complete destruction of the superior colliculus does not affect at all the light reflex. (Knoll 1869, Bechterew 1883, Bernheimer 1909, Levinsohn 1909, and Keller and Stewart 1932).

Ranson and Magoun (1933), Magoun (1935), Hare, Magoun and Ranson (1935), Magoun and Ranson (1935) confirmed the fact that destruction of the superior colliculus in the cat did not abolish the light reflex, and showed the centre of the light reflex to be in the pretectal area.

Although this pretectal area is well distinguished from the superior colliculus in animals like the cat, in man it is less clearly separated and Kappers, Huber and Crosby (1936) tend to homologize it with the deepest layers of the superior colliculus.

RETINO COLLICULAR PROJECTION

As was mentioned in the introduction, the projection of the retina on the superior colliculus has been worked out in the rat, rabbit, opossum and ferret successfully by the Marchi method, (Brouwer and Zeeman 1923, Bodian 1937, Lashley 1934 and Jefferson 1940).

Brouwer and Zeeman failed to demonstrate the localization in higher mammals as cat and monkey. It seems that the number of fibres reaching the superior colliculus from the optic tract in these animals is small and it was suggested that these fibres lose their myelin covering after entering the superior colliculus and so degeneration material could not be seen.

Apter (1945) however succeeded in mapping the retinocollicular projection in the cat by recording action potentials from the surface of the colliculus by means of surface electrodes when a small flash of light is situated in a certain point in the field of vision. She found that the temporal (uncrossed fibres) from the retina are projected to the ipsilateral colliculus and that the crossed ones to the contralateral colliculus.

Apter agrees with the workers who used the Marchi method as regards the pattern of the

localization of the retina in the superior colliculus.

In the rat, rabbit, opossum and ferret (Lashley, Brouwer et al, Bodian and Jefferson) we know that the lower half of the retina is projected on the medial half of the superior colliculus, the upper half of the retina, on the lateral half of the superior colliculus, the temporal half of the retina is presented anteriorly in the colliculus and the nasal half of the retina is caudal or posterior on the colliculus. In these animals there is more or less complete crossing of optic fibres in the chiasma, whereas in the cat there is partial decussation. So Apter found systematic projection of the temporal retina of the left eye on the left superior colliculus, of the nasal retina of the left eye on the right superior colliculus. The line of division passes through the area centralis. The lower retina is projected on the superior colliculus medial to the upper retina. Points along the vertical meridian are projected at the anterior end of the superior colliculus. Points 110° temporal to the vertical meridian of the visual field of the left eye are at the posterior end of the right superior colliculus. Points 90° nasal to this vertical meridian are at the

anterior end of the left superior colliculus.

THE SUPERIOR COLLICULUS AND OCULAR MOVEMENTS

The presence of localization of the retina on the superior colliculus and the connection of the latter with the occipital and frontal cortex on the one hand and nuclei of the oculomotor nerves on the other, makes it highly probable that the superior colliculus is concerned with fixation reflexes.

It was known that electrical stimulation of the superior colliculus produces conjugate movements of the eyes, the direction depending on the site of stimulation on the superior colliculus. This was systematically studied by Apter 1946. Her method consists of applying strychnine on a little area on the surface of the superior colliculus of cat under very light anaesthesia. The point in touch with the strychnine will of course become readily sensitive to incoming visual impulses. At this time a light is flashed into the eye. Both eyes then move together to bring the centre of gaze to a certain point in the visual field. This point in the field is then corresponding to the point on the surface of the colliculus covered or under the effect of strychnine.

The whole surface of the colliculus was thus investigated with the strychnine noting each time

where theeyes looked in the visual field. Apter thus mapped the colliculus for these movements and the map is in agreement with the previous anatomical and physiological findings.

THE SUPERIOR COLLICULUS AND OCULAR MOVEMENTS IN MAN

The afferent limb of the reflex arc for ocular movements starts in the retina and ends in the cortical visual area. The efferent link is presumed to be the corticofugal fibres passing to the superior colliculus and ultimately to the eye muscles nuclei. As concerns the reflex centre it is supposed to be in the occipital lobe. What is the function of the frontal centre then? Holmes (1938) writes "All evidence at our disposal indicates that the frontal oculomotor centre is concerned in those movements and reactions of the eyes which we may call voluntary. Through it, we can by an effort of will look or turn our eyes in any direction and converge them on a near object." On the other hand - "The functions of the occipital centre are more numerous. Fusion, that is, the reactions necessary to unify the separate impressions from the two retinae, and accomodation depend on it. The movements of the eyes to an object outside central vision in so far as it is involuntary is also excited through the occipital cortex by extra foveal impulses. And finally the maintenance of fixation on a point,

whether it is at rest or in movement is determined by a cortical reflex mechanism in the occipital lobes". It appears that the superior colliculus is involved in these ocular reflexes.

It is a basic mechanism on which impulses from both occipital and frontal centres can act. But certain observations indicate that a subcortical reflex mediated through the colliculus alone could exist, for example, the sudden turning of the head to a flash of light and occurence of optokinetic nystagmus in infants and the unconcious patients. Furthermore, there is suggestion that the retinocollicular projection in man is well localized. This is inferred from cases of pineal body tumours pressing on the superior colliculus. In these cases paralysis of gaze in an upward direction is commonly observed. This is followed later by paralysis of downward gaze and in the terminal stages of horizontal gaze. From Apter's map we find that the site for upward movements of eyes is found medially and anteriorly on the superior colliculus, and this is the part first pressed on in pineal body tumours, followed by the lateral anterior part which is concerned with downward gaze.

THE ROLE OF THE SUPERIOR COLLICULUS IN BRIGHTNESS DISCRIMINATION

Once the habit of brightness discrimination has been established in rats, then complete destruction of the striate area leads to temporary loss of the habit which can be reformed in normal learning time (Lashley 1926 - 1936). Herrick (1926) and Brown (1935) suggested that the mechanism for the habit must be subcortical. As the lateral geniculate body is effected by retrograde degeneration then it cannot be held responsible, so the superior colliculus seems to be of importance in that function. But Freeman and Papez (1930) and Laymen (1936) proved that rats with lesions in the superior colliculus could learn a brightness discrimination in the normal learning time.

So it seemed likely (Lashley 1935) that both the striate cortex and superior colliculus have equivalent importance in the habit, and so if one is destroyed the other will take over its function.

THE SUPERIOR COLLICULUS AND PATTERN VISION

Lashley (1931) and Lashley and Frank (1934) suggested that the superior colliculus may be important in pattern vision. These workers were investigating the cerebral cortex, and they showed that the anterolateral part of the striate area is essential for detailed vision in the rat. Some of the rats incidentally had lesions in the

superior colliculus together with lesions in non cortical parts of the striate area. These rats were disoriented on the jumping stand. But later Laymen (1936) found that rats with colliculus lesions alone could learn to discriminate striations as well as normal animals. Ghiselli (1937) suggests that the possibility remains that the superior colliculus might be involved in the habit in the intact animal. If there were a loss of the habit, or a reduction in visual acuity after lesions in this centre, such would seem to be the case. So Ghiselli taught a group of rats to discriminate striations and brightness. Their visual acuity and brightness thresholds were also determined. After destruction of the superior colliculus, the animals were tested for retention and their thresholds of discrimination were redetermined. It was found that the lesions produced no loss in the retention of either discrimination or change in visual acuity or brightness threshold. Ghiselli concluded that detail and brightness discrimination habits are not mediated by the superior colliculus alone.

THE CONNECTIONS OF THE OPTIC LOBE IN BIRDS

There is complete decussation of optic nerve fibres at the chiasma. Perlia (1889) demonstrated this in cuckoo, chicken and sparrow.

A great deal of attention was given to the accessory optic tracts in birds whereas very little was given to the optic tract itself. The greater number of the fibres after crossing at the chiasma incline lateralwards and slightly backwards and constitute the lateral or marginal optic tract. This enters the tectum surrounding it on all sides and forms the covering layer. It contributes small bundles to the lateral geniculate body.

Perlia traced the smaller bundle known as the medial optic tract dorsalward and found it to terminate in a nuclear mass which he termed the nucleus of the medial optic root. Perlia referring to a statement by Von Gudden that there exist two types of fibres in the optic nerve: fine centripetal fibres concerned with the light impulses arising in the retina and carrying them to the brain, and coarse centrifugal ones concerned with pupillary reactions. Perlia considered the medial optic tract as carrying the second type of fibres.

Many workers described the nucleus at which the medial optic tract ends. Bellonci (1888), Singer and Münzer (1890) and Jelgersma (1896), called it

ganglion opticum basale. Edinger (1895) called it the ganglion isthmi. Recently (1928), Craigie considered it one portion of the ganglion isthmi complex. Jelgersma (1896) after enucleating one eye, could prove that the cells in the nucleus degenerate and he regarded the optic fibres leading from it as centrifugal in character. This was further proved by Wallenberg (1898) who gave further proof of its centrifugal course by proving that direct injury to the nucleus was followed by degeneration of the tract.

It seems that the cortex of the bird has aroused so much interest that one finds most of the work done is on that structure. The visual function among other functions aroused much interest. Edinger (1895) believed that the occipital lobe of the forebrain was an optic centre and that its chief association path was the occipito mesencephalic tract. Kalischer (1900) looking for centres for movements of different organs found a centre concerned with closing of the eyes and he too considered the posterior pole visual in function. Kalischer confirmed his localizations by extirpation operations. But Boyce and Warrington (1898) found that injury to any portion of the hemisphere produced a deficiency in sight, although the defects were most marked after removal of the entire

hemisphere or removal of its occipital portion.

Birds deprived of their hemispheres sat with the eyes closed and with feathers ruffled, and manifest[ed] great lack of interest. Later they start to move and even become restless. They avoid obstacles in their way and they can maintain their equilibrium.

Recently Bremer, Dow and Moruzzi (1939), obtained a conjugate deviation of the head and eyes toward the opposite side of the stimulated cortex in the unanaesthetised pigeon, this is accompanied by constriction of the pupils and opening of the palpebral fissure.

As regards reaction to light stimulation, these authors found that the cerebral cortex of the pigeon reacts to the illumination of the contra-lateral eye by a large initial wave "on effect". There is no distinct "off effect" on cessation of the illumination.

These workers concluded from their experiments on the cortex of the pigeon that the superficial layers of neurons covering the striatum dorsally and posteriorly have physiological properties and a functional significance- the latter being essentially optokinetic, much like those of the neopallium of mammals.

A very great number of tracts coming to or leaving the optic tectum in birds has been described by anatomists (see Kappers, Huber, and Crosby 1936). The functional significance of most of them is obscure and so they are not mentioned here.

METHODS
ANAESTHESIA

Rabbit

Urethane 1gm/kgm was used in seventeen preparations. The drug was prepared as 25% in saline solution and injected intraperitonially. It took 45 minutes to put the animal under deep surgical anaesthesia with loss of corneal reflex. To hasten the effect of the anaesthetic, 1cc of the dose could be injected in an ear vein and the rest into peritoneal cavity.

When urethane was used, the above mentioned dose was usually sufficient to keep the animal anaesthetized for at least ten hours. It was rarely necessary to inject more during the experiment. The disadvantage is that it lowers the blood pressure in some animals (as judged by soft eye ball) to such an extent that the retina seems not to function. Chloralose was added to Urethane (25 mgm/kmg body weight) in one instance, but the irritability it causes to the animal even when it is fixed in the stereotaxic instrument makes it undesirable.

Ether alone (for induction and maintenance) was used once, but to induce anaesthesia with ether in rabbits is very dangerous. The animal gets into a stage of irrecoverable shock once it is roughly handled, so in four rabbits, nembutal (0.3cc for kgm body weight) diluted in saline was

injected very slowly into an ear vein and then anaesthesia continued with ether, using a pump. Animals with ether anaesthesia showed great vitality and gave excellent responses.

Goat

Nembutal was used in three preparations. In one, anaesthesia was induced with ether before nembutal was injected. The goat consumes nembutal very quickly and a full dose may have to be repeated by the end of thirty minutes. So a continuous drip was used.

For induction 1cc per 5lb body weight was injected slowly into the external jugular vein, a canula was then inserted into the vein and connected to a continuous drip infusion bottle containing a full dose (2cc per 5lb body weight) of nembutal which could be run when necessary. Apart from the short lasting effect of nembutal it lowered the blood pressure too much in some animals.

Urethane 0.5 gm per kgm body weight and chloralose 0.05 gm per kgm in saline were used in six preparations. Urethane is also consumed quickly by goats but not as quickly as they consume nembutal. Again induction was by slow intravenous injection into the external jugular vein and a venous canula was inserted. As a rule about three full doses are required in the course of the twelve hours.

Pigeon

Chloral hydrate 0.2 gm in 1cc saline injected intraperitoneally was found very successful. It was rarely necessary to repeat the dose in the course of the experiment. The safest way for injection is to insert the needle just caudal to the free edge of the sternum in the midline. Injection of chloral hydrate into the pectoral muscles is dangerous. It seems that absorption from these big muscles is too rapid and quickly kills the animal. Intravenous injection (axillary vein under the wing) is extremely difficult with such a big volume of fluid. The vein wall seems to be so friable that even with the best precautions one will always get a haematoma. For decerebration, used ethyl chloride and ether and this was very successful. An easy way for administration is to put cotton wool soaked with the anaesthetic in the bottom of one litre beaker and put the beaker on its side and slowly push the pigeon inside it, when it can be seen through the glass to be affected by the vapour in few minutes.

The maintenance of an adequately high blood pressure

For the retina to respond to visual stimuli it was found that a normal blood pressure must be maintained. Unfortunately with the anaesthetics used, except ether in the rabbit and chloral hydrate in the pigeon, the preparations suffered from low

blood pressure expecially in the late hours of the experiments. This was a genuine effect of the anaesthetic and not from haemorrhage. Once the blood pressure drops the pupils dilate enormously and the intraocular tension becomes very low as judged by softness of the eye-balls to palpation. In the rabbit a small dose of dextran (5cc) was in most cases effective in maintaining an adequately high blood pressure, but it often had to be repeated. With the goat it was even more complicated. When under anaesthesia the goat salivary secretion was pouring all the time and so a continous adminstration of saline had to be maintained to combat the anhydraemia, and often a repeated injection of dextran was needed.

In the goat a wide needle had always to be inserted into an intestinal loop to allow gas out, otherwise respiration is seriously effected.

OPERATIVE PROCEDURES

Rabbit

A tracheal canula was always inserted. The scalp was incised and in the first preparations a trephine hole was made on one side of the midline to avoid the superior longitudinal sinus. The hole was enlarged with the bone nibblers till a good exposure of both occipital lobes was obtained. Later the trephine was discarded and a dental burr was used to open the skull. This was very safe and did not injure the venous sinuses nor the dura.

Plasticine was found to be the best method to stop bleeding from bone edges, and fibrin sponges were frequently used to stop bleeding from soft tissues. In a few instances suction was used to remove the occipital lobes. This entailed quite a big amoung of bleeding.

The external auditory meatuses were then exposed either through the same scalp incision or through a lower separate one on each side.

Goat

The same procedures were followed except that the trephine was never used. The dental burr was always used instead. In later experiments when the goats in stock became older the horns had to be amputated which led to a profuse bleeding, but easily stopped with plasticine.

The dura was usually kept intact till the animal was mounted on the stereotaxic instrument and then it was incised using a sharp cataract knife.

Pigeon

Same procedures were applied, but the skull of the pigeon is very brittle and the bone is packed with air cells so one has to be careful when using the trephine or dental burr. Another difficulty was the presence of a bony tentorium which encroaches on the posterior part of the upper surface of the optic tectum. It was found best to remove it

piecemeal very slowly with a pair of stout sharply pointed forceps. One should never forget this bony shelf if going to insert needles into the optic tectum otherwise the needle tip is broken. For decerebration a small spatula curved on the flat was used (Fig. 1). After removal of the hemispheres the anterior part of the cranial cavity had to be well plugged with fibrin sponge otherwise the base of the brain would be covered with a pool of blood.

No incision was needed to expose the auditory meatuses because they are on the surface in the pigeon.

Curare (0.15 mgm.) is always needed after decerebration to prevent the animal from flying. It was injected into the pectoral muscles.

MICRONEEDLE ELECTRODES

Steel needles were used. The thicker the occipital lobe (as in goat) the longer the needle. The needles were sharpened on Arkansas stone mounted on a motor, till the tip was five microns thick. It was found that needles thinner than five microns at the tip easily break while traversing the occipital lobe.

After sharpening, the needles were cleaned carefully with trilene to remove oil and dirt, then dipped in varnish and slowly but steadily withdrawn and

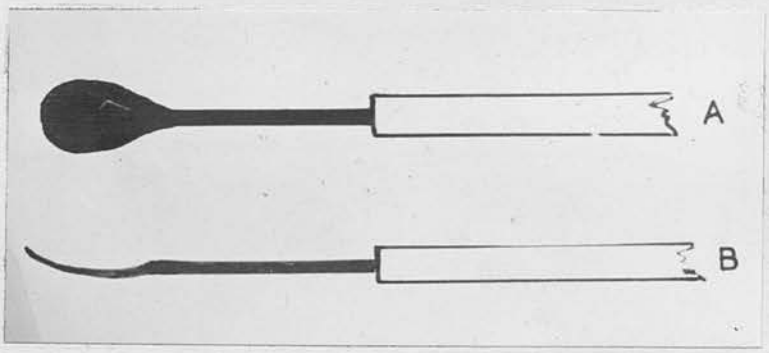


Fig. 1 shows the spatula used for decerebrating the pigeon. A. shows the flat end of the spatula. B. shows the spoon-like curve as looked at from the side.

baked in an oven at 210° C for ten minutes. This was always repeated so that each needle would have two coats of varnish. The insulation of the needle was tested by using a 1,000 c/s oscillator note, a wet sharpened match stick covered with wet cotton wool and a pair of head phones. A good needle has to be covered with varnish all over except the very tip and base which will be in contact with the tissues and the needle holder respectively.

STEREOTAXIC INSTRUMENT

The head of the animal was clamped in a stereotaxic head holder, over which the needle holder was attached to the micrometer scale. Ear-pieces plugged into the external auditory meatuses, and a bar to support the upper jaw or beak were used for the rabbit and the pigeon and in addition to this a nailed side piece on each side was screwed into the face bones of the goat.

In most animals the external auditory meatus is straight and may be directed horizontally inwards as in the cat and monkey or forwards as in the goat. For the goat a special head holder has to be used with the arms carrying the ear pieces directed inwards and backwards at an angle of 45° with the midline (Fig. 2) but the ear pieces are the same (Fig. 3).

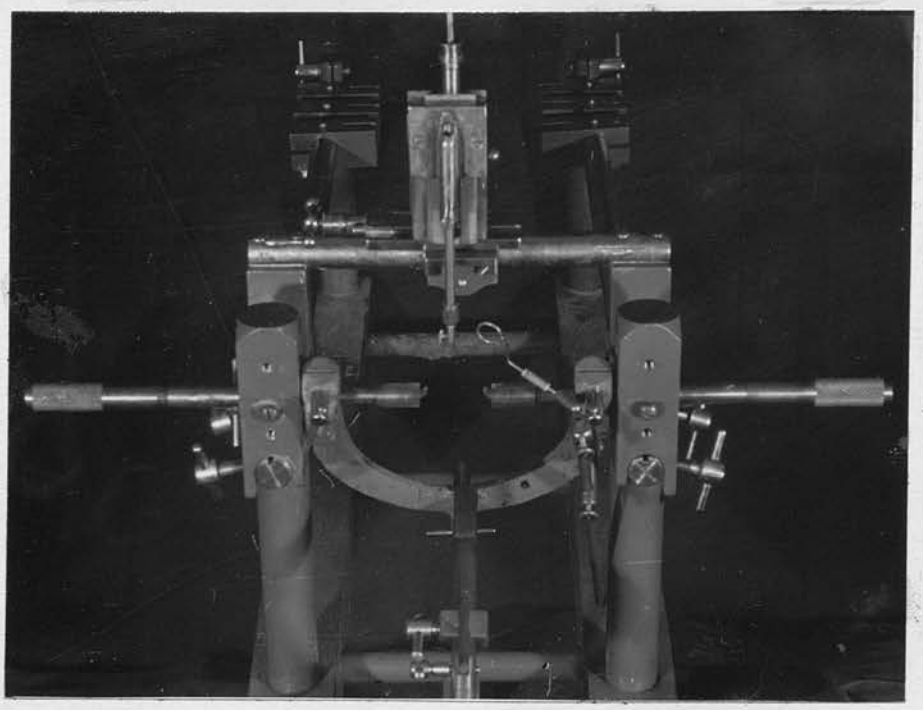


Fig. 2a Photograph of steriotaxic head holder used for rabbit and pigeon. Ear pieces of rabbit are shown and also the ring for fixing the eye .

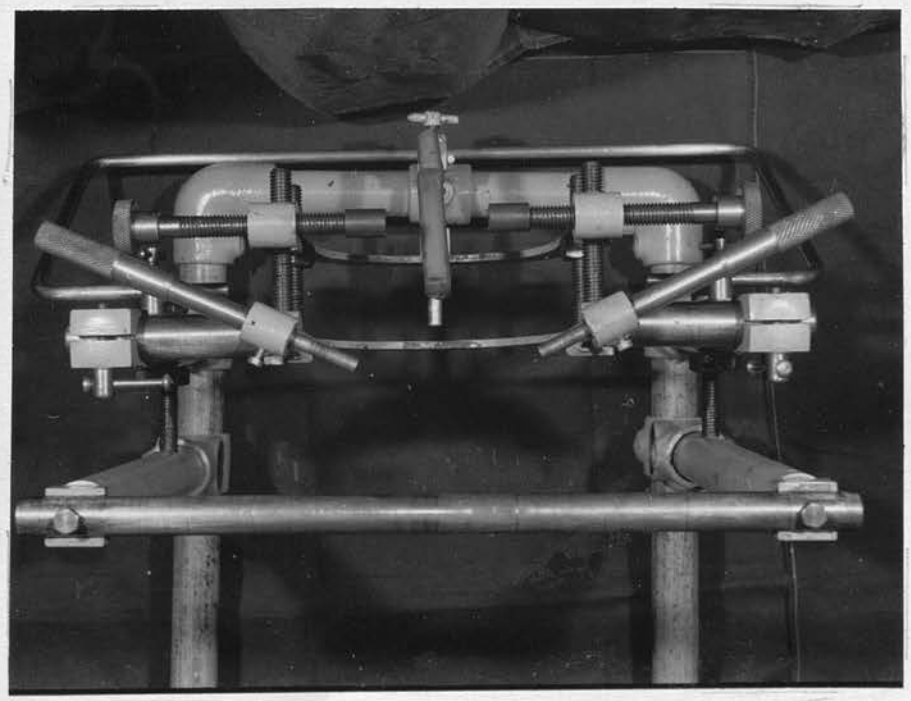


Fig. 2b Photograph of the steriotaxic head holder for the goat , showing how the arms carrying the ear pieces are directed inwards and backwards at an angle of 45° with the midline. The instrument is looked at from above.

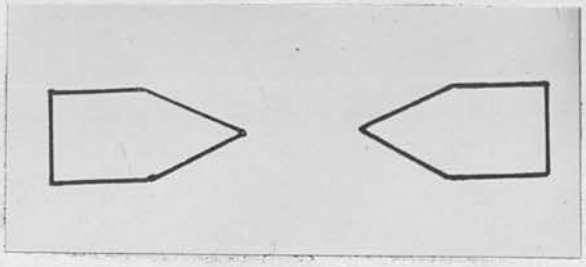


Fig. 3 shows the conical ear-pieces used for the goat and pigeon.

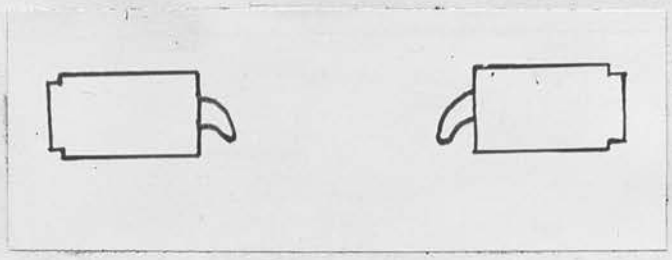


Fig. 4 shows the ear-pieces used for the rabbit

Conditions are quite different in the rabbit. In fact it is the most difficult animal to fix on the stereotaxic instrument. Actually an animal held in the instrument is supported mainly by the ear-pieces. In the rabbit the external auditory meatus runs inwards for a very short distance and then downwards for a considerable distance. If one uses the ordinary ear-pieces which do well for the cat, monkey, goat and pigeon they will simply penetrate the thin shell of bone and compress the brain stem, and the animal dies. A mould of the meatal cavity of the rabbit was prepared and attached to the free end of the ear-piece and by inserting them in the cavities and applying very carefully sufficient pressure by screwing the arms of ear-pieces inwards one could hold the head in place (Fig. 4). As mentioned before the external auditory meatuses of the pigeon are quite superficial and run horizontally inwards. The conical ear-pieces were used very successfully.

As regards the support for the upper jaw, a bar was used with a groove to lodge the two central incisors in front, while the part of the bar inside the mouth should fill the palatine arch. Again there was modification for the rabbit because it has two rows of incisors, long ones in front and stunted ones behind. Special grooves were made to accomodate both (Fig. 5).

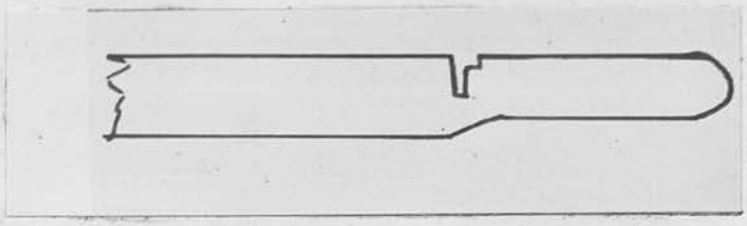


Fig. 5 the bar used to support the upper jaw of rabbit showing the two grooves for accomodating the anterior long and the posterior stunted incisors.

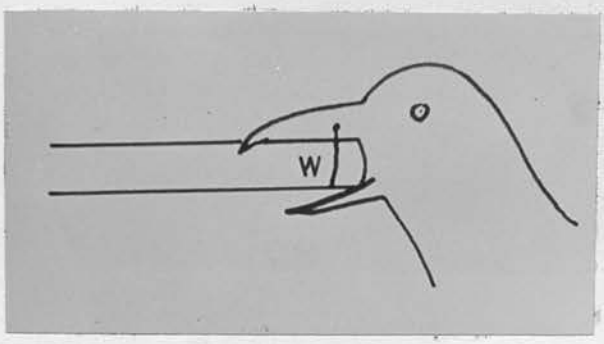


Fig. 6 the bar used to support the upper beak of the pigeon showing the groove to accomodate the curved tip of the beak and the steel wire passing through the nares and around the bar.

In the pigeon the upper beak was rested on the bar with a shallow groove to accomodate the downwards curve of the tip of the beak and a soft steel wire is passed from one nare to the other, and around the bar to hold the beak tightly in position (Fig 6).

THE RECORDING SYSTEM

This was a conventional resistance capacity coupled amplifiers with differential input. The indifferent electrode was put in inactive scalp tissue. Two cathode-ray tubes, one for observation and one for camera were used to give visual records while a loud speaker gave auditory records.

The stimulus was a small interrupted neon flash with a diaphragm having a hole of 1mm. diameter. This subtends an angle of 0.25° on the retina. The stimulus could be mounted on the arms of the perimeter and moved on it.

REFRACTION

Both rabbit and goat were refracted under atropine cycloplegia. The rabbit was found to be emmetropic while the goat is myopic (-2) dioptres. Even with the myopia of the goat the distance of the stimulus from the eye was not long enough to cause any distortion of the image.

FIXATION OF THE EYE

To obtain accurate results in the mapping of the retina on the superior colliculus the eye had to be fixed all the time and centred to the fixation point on the perimeter. For fixation of the eye a brass ring with an arm attached to one of the pillars of the stereotaxic instrument was used. The ring was stitched to the eye ball around the cornea. For the stitches to be of value they must be corneal or in the conjunctiva in the very near vicinity of the limbus as it is the only place where the membrane is adherent to the sclera. If stitches are inserted even a few millimeters from the limbus they are quite useless as the eye could still move freely.

Brass rings of different diameters were made for the goat, rabbit and pigeon.

If muscles were desired to be tested by pulling on them they were detached from their scleral insertion and tied to a string before inserting the brass ring.

The fixed eye always had a lower intraocular tension than the free one. It was first thought that this resulted from interference with the circulation in the arteries of the ciliary muscle when the extra ocular muscles were handled, but later it was found that this lowering occurred

equally in preparations where the muscles were left intact. Anyhow, provided the blood pressure of the animal was about normal this unilateral low intraocular tension did not interfere with retinal responses to visual stimuli.

As regards centering the eye, the optic axis was used as a guide. The visual axis could not be used because there was no co-operation from an animal under anaesthesia nor was it possible to see a macula on which to centre the perimeter on. In fact one cannot recognize a macula in the rabbit either ophthalmoscopically or by dissection, and the goat has a very dim light reflex which made conditions very difficult as regards recognizing a macula by ophthalmoscopic means. The pigeons eye was too small to apply such a procedure to.

Light was received from above on to a glass slide placed opposite the hole of the centre of the perimeter with such an angle that the rays would be reflected into the animals eye. Looking through the hole in the perimeter behind the glass slide and manipulating the brass ring whose arm is attached to a movable ball and socket joint one could always fix the eye in a position that the image of the reflected light is in the centre of the pupil, whether it is the round pupil of the rabbit and pigeon or the horizontal one of the goat (Fig.7).

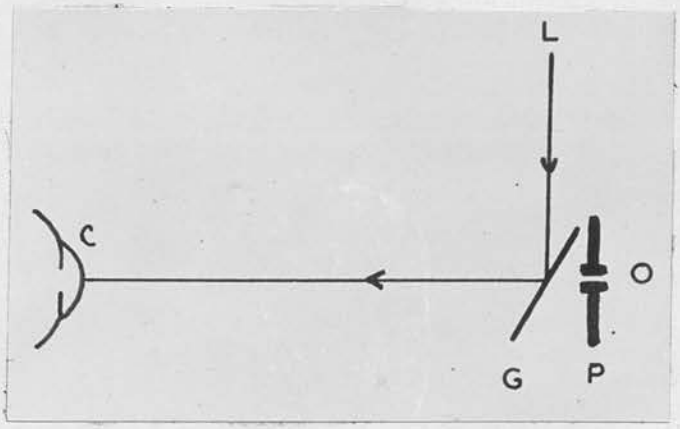


Fig. 7 shows how the eye was centred on the fixation point on the perimeter

O. observer's eye looking through hole in centre of perimeter P.

L. source of light

G. glass slide set obliquely

C. animal's eye

THE PERIMETER

A brass perimeter nine inches in radius was used. The centre was always nine inches from the cornea. The stimulus could be mounted on the arm of the perimeter and moved on it. When the needle was in the colliculus a big light was flashed near the eye and an approximate idea was formed about the point in the field which would give a response. The big light was then carried away from the eye towards the perimeter and finally replaced by the small stimulus. At first the response was localized (as will be seen later) and when the needle was deeper than the surface one could record from a wider area in the field and so every 5° meridian was tested in the area of response and recorded the extent on that particular meridian on a chart of the field of vision.

Difficulties in perimetry

A disadvantage in the stereotaxic instrument used, was that it had a pillar which was so near to the eye and interfered with a great part of the lower temporal quadrant of the field and to a lesser extent with the upper temporal quadrant, but fortunately not with the posterior horizontal plane near the centre of the perimeter, so that the central field could be investigated thoroughly.

To ascertain the results from these inaccessable territories a mirror was placed behind the eye with its long axis cutting the posterior horizontal plane of the perimeter at 25° from the centre. When light was flashed from the anterior arm of the perimeter it fell on the mirror and would appear to the eye of the animal as if it were coming from somewhere in the temporal field. This part of the investigation was started after a good deal of the superior colliculus of the rabbit had been investigated, so it was possible with the help of measurements with the stereotaxic micrometer to insert the needle in the projection area of the temporal field so as to get response from this field. To make sure that one was not recording response from the stimulus itself but from its image, in each stab, the eye was covered in such a way that it could not see the actual stimulus but could see the image in the mirror and response was always obtained whereas if one left the stimulus free and covered the mirror the response immediately disappeared.

To calculate where the response exactly came from in the temporal field actual drawings were made of the perimeter and the reflexion of the light on the mirror was constructed. It was found that with the position of the mirror inclined 25°

on the perimeter and very near to the eye that

$$A = 50 + B$$

where B is the angle at which the light stimulus was placed on the anterior arm of the perimeter and A is the angle on the posterior arm of the perimeter and hence the would be position of the stimulus in the temporal field.

HISTOLOGICAL METHODS

After the completion of each experiment the brain of the rabbit or goat was perfused with saline to wash out blood and then with 10% formaldehyde. In the case of the pigeon the optic tectum was put in a 10% formaldehyde solution for four days.

The superior colliculus was cut into sections and stained to detect the needle tracks. At first Cajal's silver staining method was used but soon was given up because it was very slow and as the sections are frozen each had to be stained separately and kept all the time in a separate numbered glass container.

The Weil stain with embedding in nitrocellulose lower viscosity (NLV) was quite adequate for detecting the needle tracks, because it took a short time and each section could be numbered.

20% solution was prepared as follows:

NLV	140 gm
Absolute alcohol	210 c.c.
Anaesthetic ether	250 c.c.
Celloidin	4 gm

Celloidin was dissolved in alcohol ether first. When completely dissolved NLV was added. The solution was stored in a wide mouthed bottle with ground stopper.

5% solution was prepared by diluting one part of 20% in three parts of alcohol ether equal parts. 10% solution was prepared by diluting 20% in equal parts of a mixture of alcohol ether (equal parts).

The tissue was then dehydrated. If just immersed in the dehydrating agents it would take three days to dehydrate it, so instead a small rotator was used and for a small piece of tissue as the superior colliculus the whole dehydration could be completed in six to nine hours. So after fixation the tissue was dehydrated in 75% alcohol in the rotator for two to three hours at 120 revolutions per minute. Then in absolute alcohol for two to three hours at 120 revs. per minute. Then alcohol ether equal parts for two to three hours at 120 revs. per minute. Then in 5% NLV for two to three hours at 100 revs. per minute. Then in 10% NLV for two to three hours

at 80 revs. per minute. Then in 20% NLV for two to three hours at 40 revs. per minute.

The tissue was then embedded in 20% NLV in a paper box made of finely porous paper (glazed paper should not be used) for 24 hours under a glass funnel. It should not be exposed to sunlight nor should it be allowed to dry excessively.

Marking ink was prepared by dissolving nitrocellulose in amyl acetate and coloured to correct degree with ivory black oil pigment.

The block was trimmed and the tissue was left with enough space for writing the numbers. Then the block was immersed in 20% NLV and immediately put on a wooden block which was to be fixed in the microtome. If shallow grooves are cut on the wooden block these will fix the NLV block firmly and minimize the risk of separation during cutting. It took about half an hour for the block to get firmly attached to the wood. Sections were cut 100 microns thick with the angle of knife at 25° to 45°. All the time during cutting the block was moistened with 80% alcohol to prevent drying and shrinkage. The numbering could be writen on the block in one of the corners before cutting, but sometimes this leaves a mark on the next section so it was found much easier and safer to write after cutting the section while it is still on the knife. This never failed.

To find the needle tracks much depends on how to balance the block on the microtome. One had to imagine how the needles went through and then using a landmark as for example the midline between the two colliculi, would place the block in the microtome in such a way that the knife will cut in the same plane as was the direction of the needles.

Staining

1. Sections placed in iron hematoxylin for twenty to thirty minutes.

Iron hematoxylin

Distilled water	4.5 c.c.
Alcohol hematoxylin 10%	0.25 c.c.
Iron alum 4%	5 c.c.

2. Rinsed in two changes of distilled water.
3. Differentiated in 4% iron alum. Differentiation controlled under the microscope.
4. Rinsed in two to three changes of distilled water.
5. Rinsed in 90% alcohol.
6. Placed on slide in 96% alcohol and covered with a thin paper and rubbed gently with the forefinger to flatten the sections.
7. Repeated in absolute alcohol.
8. Repeated twice in xylol.
9. Mounted quickly in dammar, and covered with a glass cover.

It was found that equally good results were obtained whether young or old hematoxylin was used. Iron alum continues to act for a longer time than one expects if the sections are not thoroughly washed in distilled water after the differentiation. It was found best, after the required differentiation had been achieved to leave the sections in a large volume of distilled water over night before they were mounted.

After dehydrating the sections it was found that the simplest and safest clearing was by xylol. The practice of using a list of chemicals as xylol-toluol, chloroform, creosote.....should be condemned.

As the sections are very thick (100 microns) much dammar had to be applied before putting the cover slip and great care was taken not to allow air bubbles to stay inbetween or below the sections. After the sections were dry they were put in the enlarger and projected on bromide paper at the required enlargement. Ten times enlargement was used for the rabbit and pigeon and five times for the goat. The needle tracks in the stained sections take different appearances. If a haemorrhage occurred the track will be seen full of blood. It may appear as a black line with a haze around it, probably due to pressure on cells

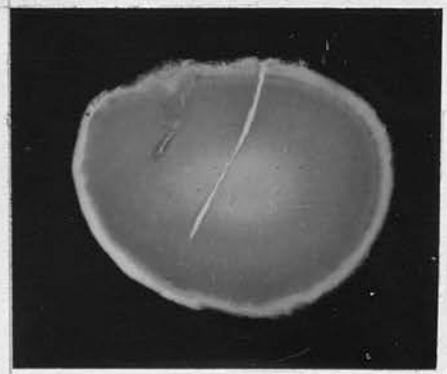
surrounding it. It may appear as an empty space (Figs. 8, 9 and 10).

Other histological methods used for studying the structure of the superior colliculus were the toluidine blue stain for the cells. Weil with paraffin sections showed excellent results, as did De Castro silver impregnation method and Roger's silver stain.

Caudal.

Rostral.

Fig. 8a sagittal section in optic tectum of pigeon in the region of the ventricle showing two needle tracks.



Caudal

Rostral

Fig. 8b sagittal section near the lateral edge of the optic tectum of pigeon showing two needle tracks

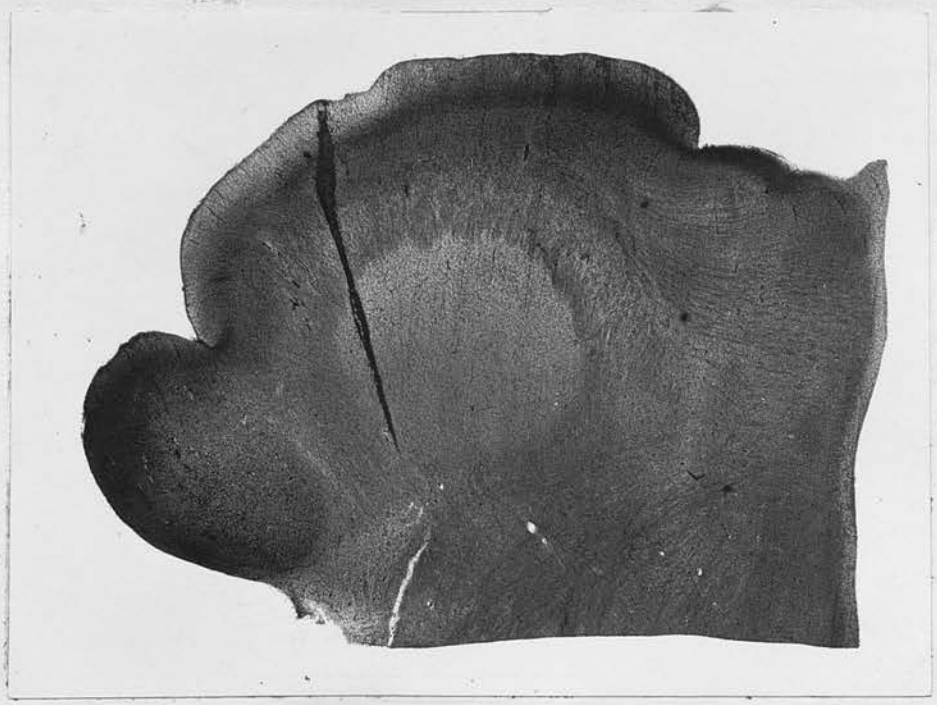


Fig. 9 Photograph of a sagittal section of superior colliculus of rabbit showing one needle track full of blood. x10

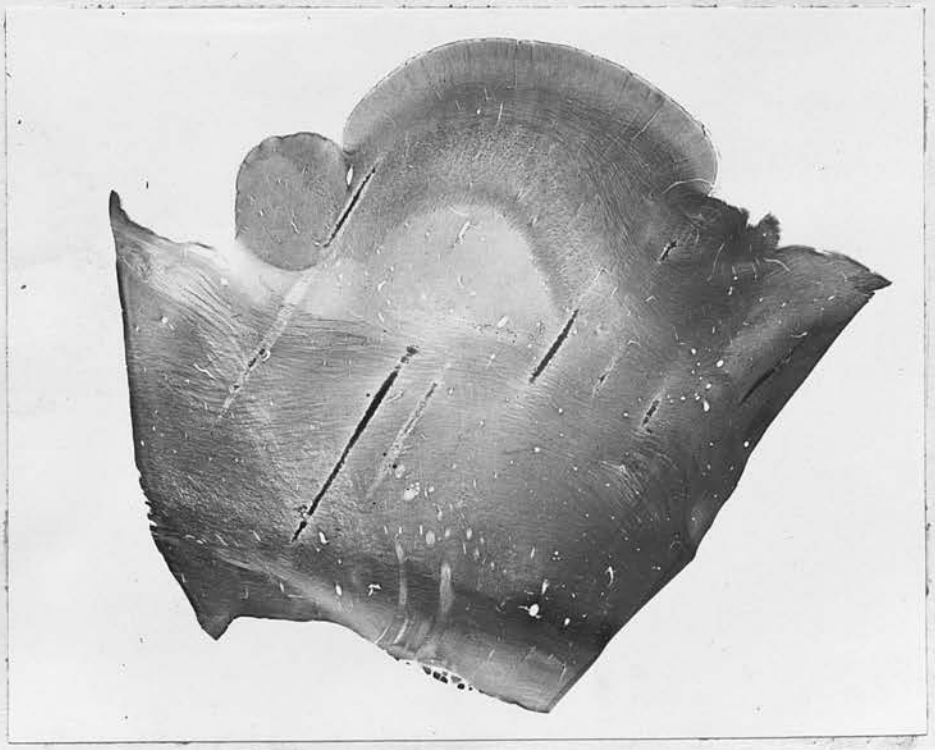


Fig. 10 Photograph of a sagittal section of superior colliculus ofgoat showing four needle tracks going deep in the colliculus and three tracks in pretectal region. x5

RESULTS

Rabbit

Twenty-three preparations were made. Eight were failures. Out of these eight two died from compression on the brain by the ear-pieces while mounting the animal on the stereotaxic instrument (Rabbits 7 and 10). Two died from haemorrhage (Rabbits 4 and 11), one from bone wound (possibly one of the venous sinuses was injured) and the other while trying to amputate the occipital lobe. Two died from unexplained low blood pressure which developed suddenly (Rabbits 5 and 22). Two were in excellent condition (Rabbits 7 and 9) but gave no response. Amblyopia was suspected and since then only animals with brisk light reflex were used.
All the failures were under urethane anaesthesia.

Altogether one hundred and three stabs into the superior colliculus were made. Only those which gave visual responses that could be seen on the screen and heard by the loud speaker and whose needle tracks were identified histologically, were considered successful. These were sixty-seven. The thirty-six remaining ones were disregarded completely either because they gave no or doubtful visual response, or they were not in the superior colliculus due to errors in using the scale of the stereotaxic instrument. Anyhow the chance of

error in using the scale was small and not more than 1mm, for example some stabs intended for the posterior edge of the superior colliculus hit the inferior colliculus. These gave auditory response.

- Two stabs recorded "collicular alpha rhythm" but the inhibition to the light stimulus was not localizable. These too were disregarded. In two early preparations no attempt was made to investigate the deeper structures of the superior colliculus, but in the later ones almost all the successful stabs were patiently investigated all through the depths of the needle tracks.

The mapping of the surface was easy and the moment the needle tip touched the surface of the colliculus and a response localized from the visual field, this was recorded and then the needle carried down to deeper layers.

From the surface of the colliculus the response was always localized and in some striking instances a slight movement of the light source to one or other side or up and down for one or two degrees on the perimeter made the response disappear.

Conditions were quite different when the needle tip was below the surface of the colliculus where no more point localization is existing. Deeper than the surface of the colliculus, response from the visual

field was usually complicated. Different shapes were noticed and they all came under one of the following: See figure 12

1. Round patches
2. Oblong or oval patches
3. Sectors with apex pointing towards fixation point. These were simple or composite
4. Narrow arcs concentric with the fixation point
5. Broad arcs also concentric with the fixation point
6. Combination of two or more of the above mentioned patterns

It was considered important to know from which layers of the superior colliculus these different patterns come. So referring to the depth from which the needle tip picked up the response and allowing in the calculation for the shrinkage which the tissue suffers in process of dehydration prior to cutting the sections the following tables were prepared containing details of twenty of the successful stabs and accompanied by diagrams from the actual photographs of the stained sections which show the particular needle track. The point on the surface of the colliculus where the needle entered is also shown.

RETINAL PROJECTION ON THE SURFACE OF THE SUPERIOR COLLICULUS

The lower half of the retina or upper half of visual field is projected on the medial half of the

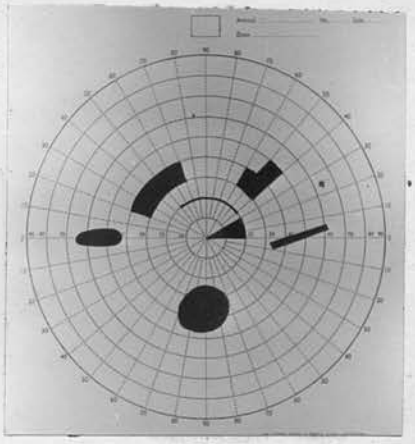


Fig. 12. Shows examples of different patterns in the visual field from which response to light stimulus could be obtained when the needle tip was deeper than the surface of the superior colliculus.

superior colliculus, the upper half of the retina or the lower half of the visual field is projected on the lateral half of the superior colliculus; the temporal half of the retina or nasal half of the visual field is projected anteriorly on the colliculus while the nasal half of the retina or temporal half of the visual field is projected caudally on the colliculus (Fig. 13).

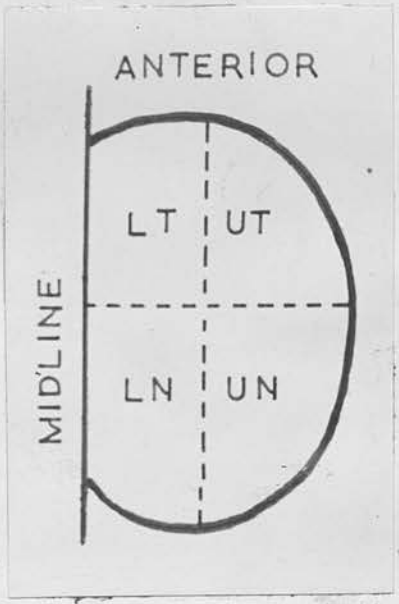


Fig. 13 shows projection of the different quadrants of the left retina on the right superior colliculus of the rabbit.

LT: Lower temporal

UT: Upper temporal

LN: Lower nasal

UN: Upper nasal

However the distribution of the visual field on the surface of the superior colliculus is not equal in terms of central and peripheral fields. The central visual field from the centre of the perimeter to 35° either on the horizontal plane or the vertical plane bisecting this centre, occupies a much larger area on the surface of the colliculus compared with the peripheral field. This is especially apparent anteroposteriorly (horizontal plane) than from side to side (vertical plane) (Fig. 14). To illustrate this, several needle stabs and their representations in the field of vision were chosen (see Figs. 14 and 15). This wide area of representation corresponds with an area of the retina surrounding the point where the optic axis falls on the posterior pole of the eye. In fact in these preparations the eye was fixed in such a way that the optic axis would be in line with the centre of the perimeter as was mentioned before. This was unavoidable as there is no macula to be seen in the retina of the rabbit either by gross dissection or ophthalmoscopically. By using the ophthalmoscope one could only see the very dim red reflex and white band of myelinated fibres running horizontally in the upper posterior segment of the eye ball, this of course is the optic papilla or blind spot. The accuracy

in mapping depends to a large extent on the fixation of the eye. Some false results were obtained in the early two preparations when the eye could be seen roving even under the deep urethane anaesthesia.

One could not obtain any visual response by shining the light into the eye on the same side of the colliculus as the needle.

In analysing the results, the upper three layers (which receive the optic fibres) were considered separately. The lower strata of the colliculus were not considered individually but as one layer from which the efferent pathway starts.

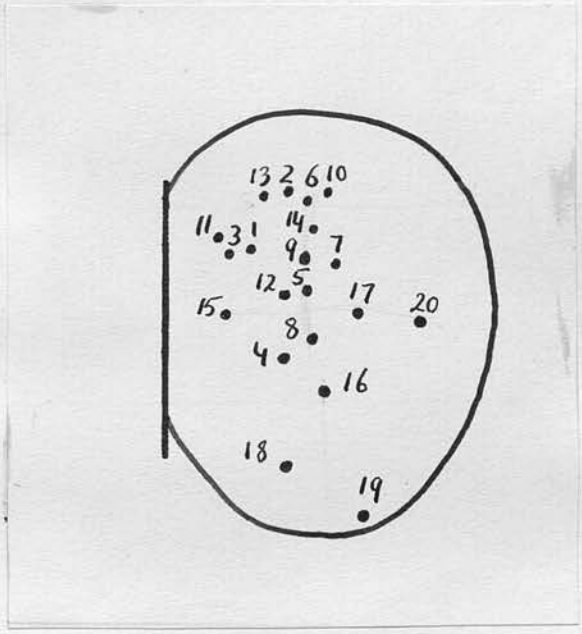


Fig. 14. Diagram of right superior colliculus of rabbit looked at from above, showing positions of needles (from different animals). The corresponding points in the visual field are shown in Fig. 15.

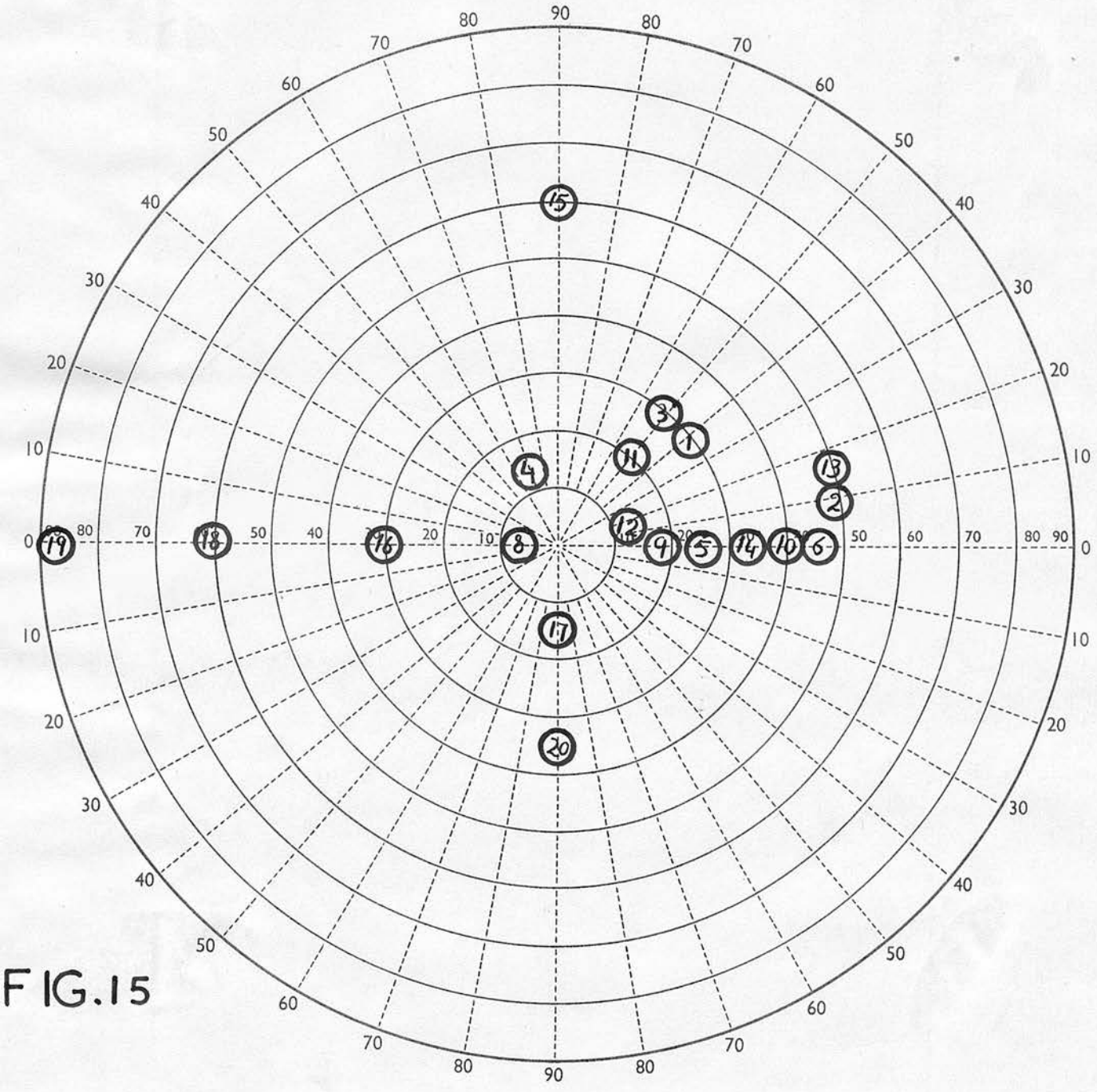


FIG. 15

Fig. 16 has been omitted

No.	R.	Anaesth.	Response from S.Z.	Response from S.G.S.	Response from S.O.	Response from deeper layers
1	8	Urethane	localized	oblong patch	unlocal-izable	none
2	8	Urethane	localized	oblong patch	oblong patch	faint
3	12	Urethane	localized	arc	faint	faint
4	12	Urethane	localized	arcs -thin -thick sectors	compound figures	faint
5	12	Urethane	localized	oblong patch	oblong patch & sharp band	faint
6	12	Urethane	localized	oval with long axis vertical	none	none
7	13	Urethane	localized	straight line and oblong patch	none	none
8	13	Urethane	localized	small arc	round patch	faint
9	14	Nembutal Ether	localized	oblong patch	none	none
10	14	Nembutal Ether	localized	oval	oblong patch	faint
11	15	Nembutal Ether	localized	oblong patch	faint	none
12	15	Nembutal Ether	localized	straight lines thin and thick	faint	none
13	15	Nembutal Ether	localized	thick arcs	?	?

No.	R.	Anaesth.	Response from S.Z.	Response from S.G.S.	Response from S.O.	Response from deeper layers
14	16	Nembutal Ether	localized	oblong patch	faint	none
15	17	Nembutal Ether	localized	oblong patch	none	none
16	17	Nembutal Ether	localized	very thick arc	very thick arc	none
17	17	Nembutal Ether	localized	compound figure	none	none
18	17	Nembutal Ether	localized	thick line	compound figure	none
19	17	Nembutal Ether	localized	thick arc	thick arc	none
20	18	Nembutal Ether	localized	compound figure	compound figure	none

R: Rabbit

S.Z: Stratum Zonale

S.G.S: Stratum griseum superficiale

S.O: Stratum opticum

The following diagrams consist of the outlines of the sagittal sections of the superior colliculi of rabbits. Marks are put to show where the responses were obtained from. An open circle on the surface indicates a localized response from stratum zonale. The point of entrance of the needle is shown as a circle on the outline of the superior colliculus. This is followed by charts of the visual field showing where the response came from. Each chart has a mark at the top which is identical with the one on the sagittal section where the response was obtained.

S.G.S. stratum griseum superficiale

S.O. stratum opticum

I.C. inferior colliculus

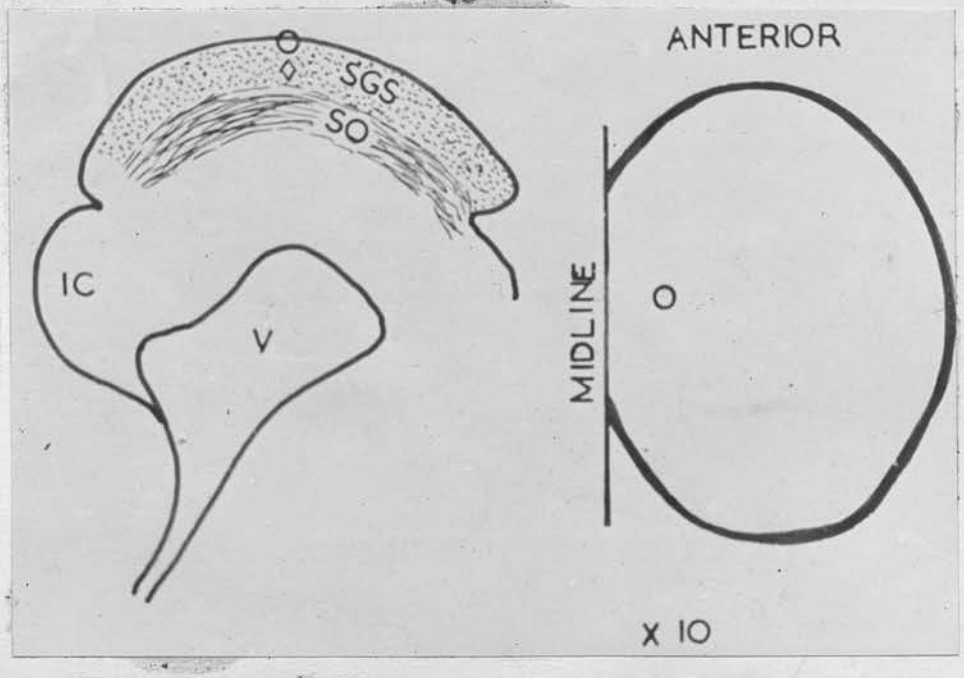


Fig. 17 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 1 in the tables). The areas in the field of vision are in the following charts. Figs.18 & 19.

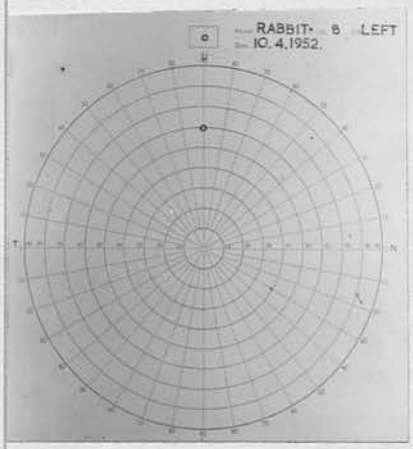


Fig. 18

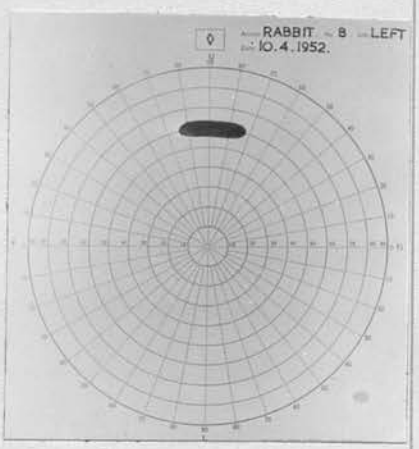


Fig. 19

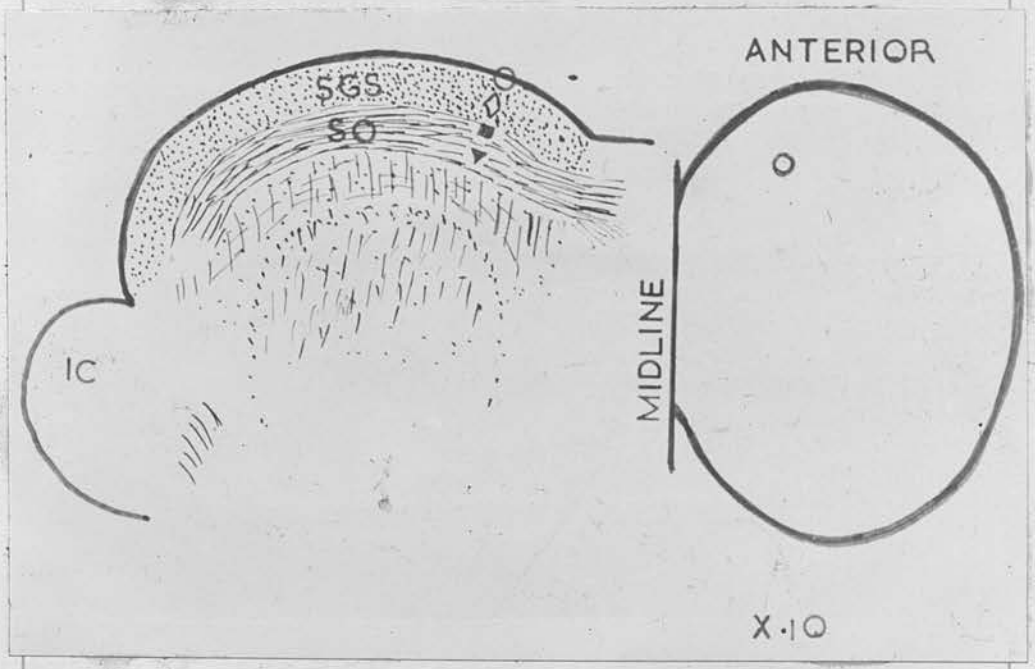


Fig. 20 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 2 in the tables). The areas in the field of vision are in the following charts. Figs. 21,22,23,24.

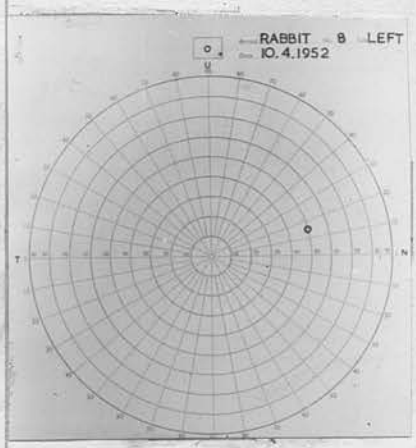


Fig. 21

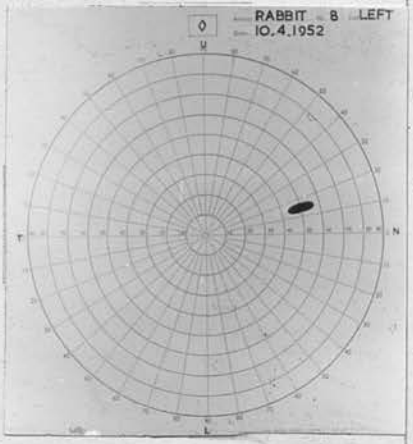


Fig. 22

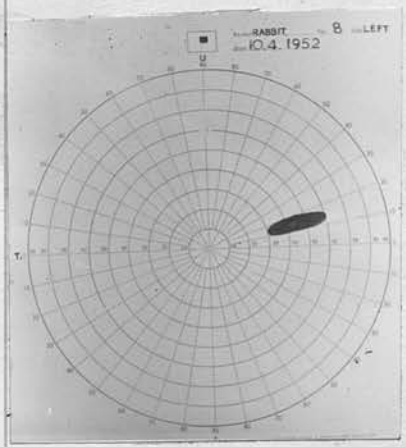


Fig. 23

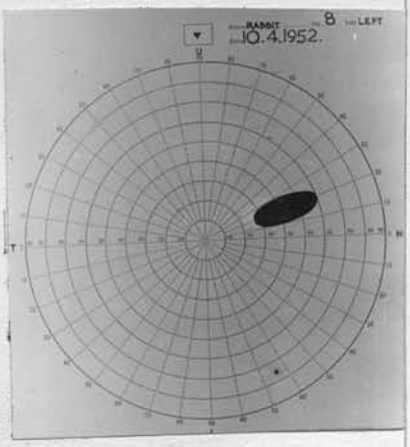


Fig. 24

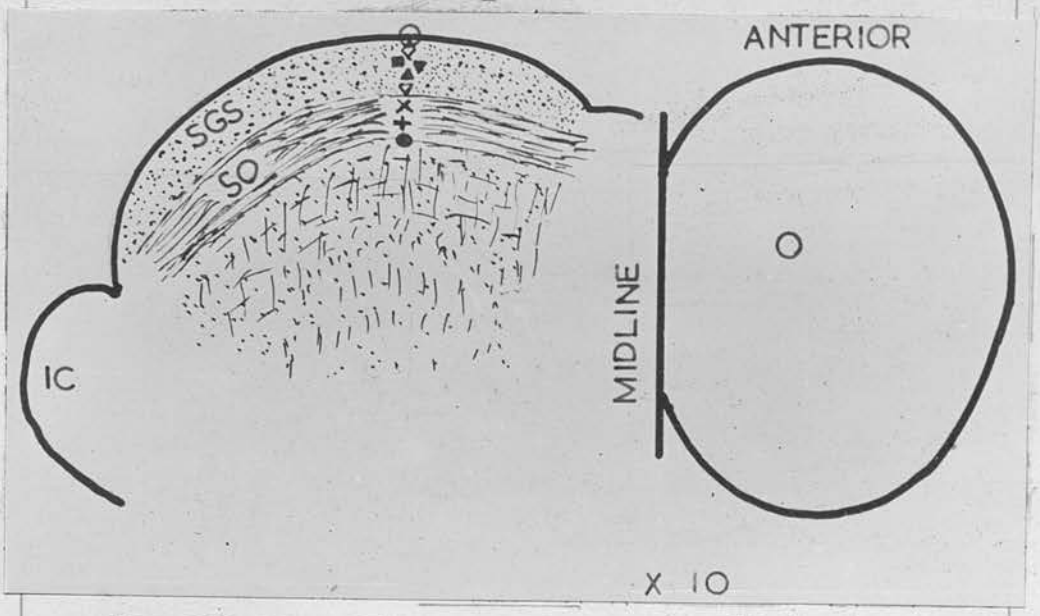


Fig. 25 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 4 in the tables). The areas in the field of vision are in the following charts. Figs. 26, 27, 28, 29, 30, 31, 32, 33.

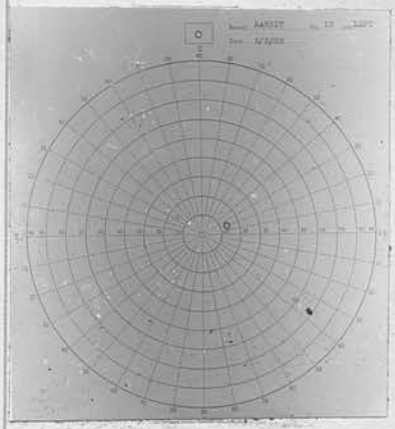


Fig. 26

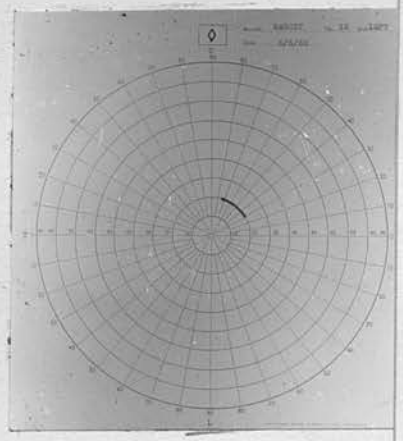


Fig. 27

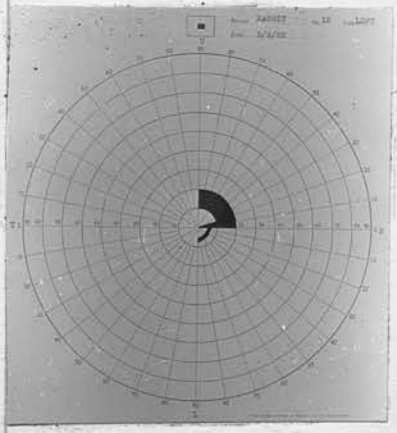


Fig. 28

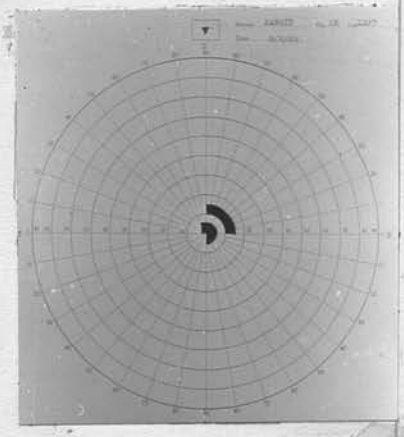


Fig. 29

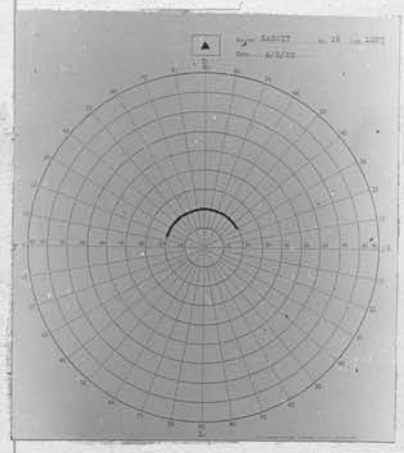


Fig. 30

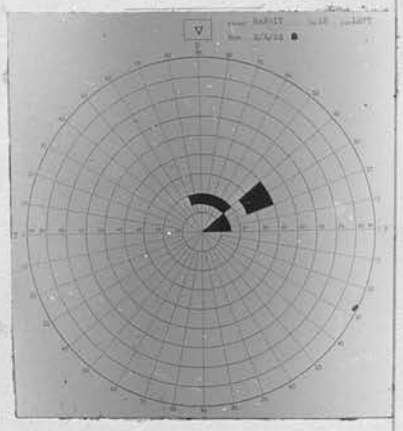


Fig. 31

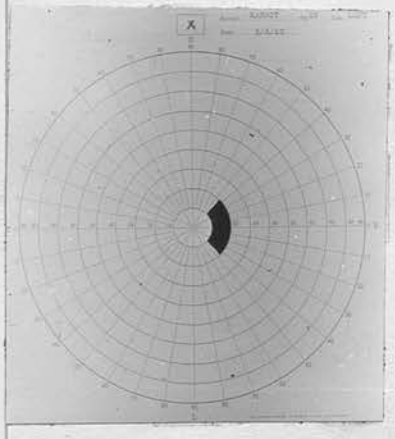


Fig. 32

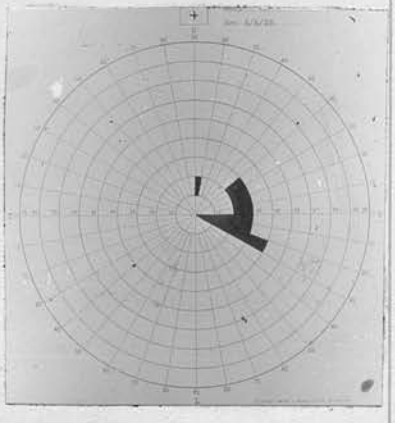


Fig. 33

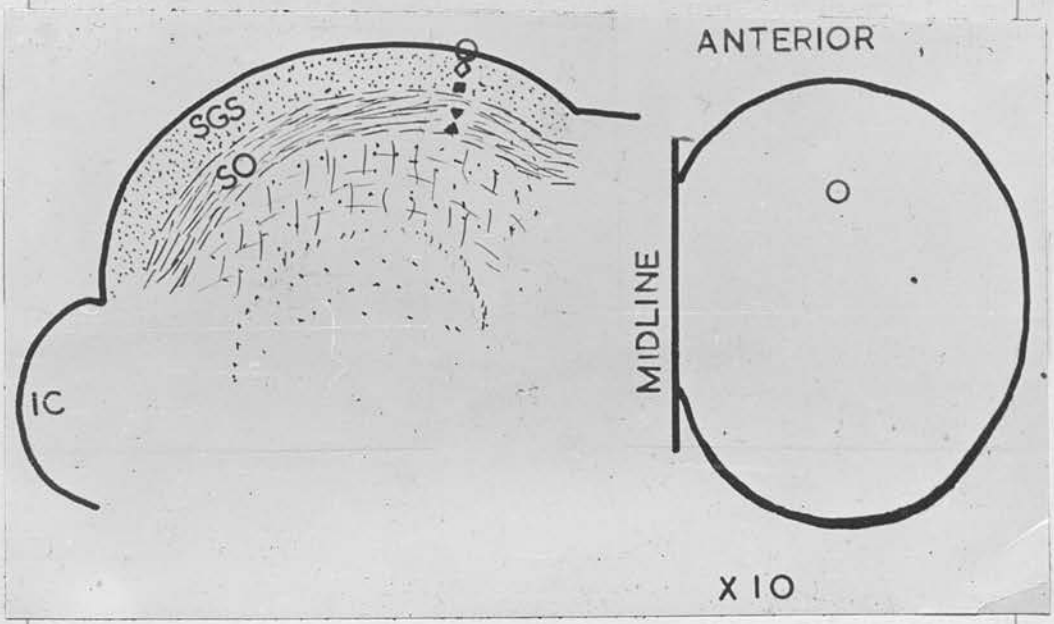


Fig. 34 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 5 in the tables). The areas in the field of vision are in the following charts. Figs, 35, 36, 37, 38, 39.

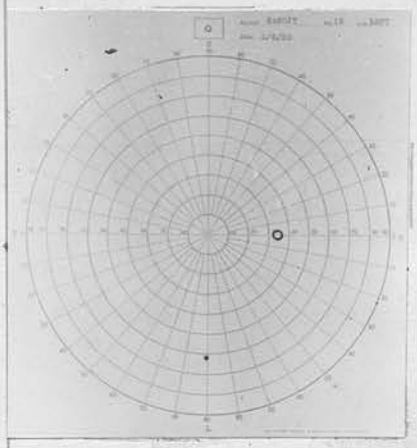


Fig. 35

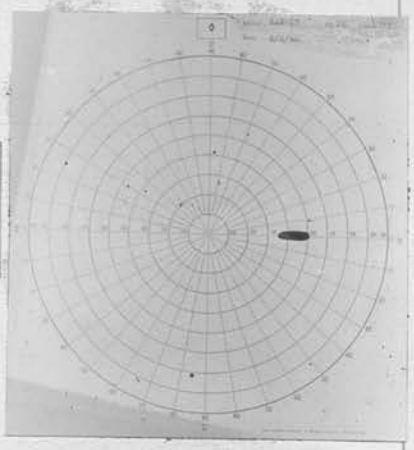


Fig. 36

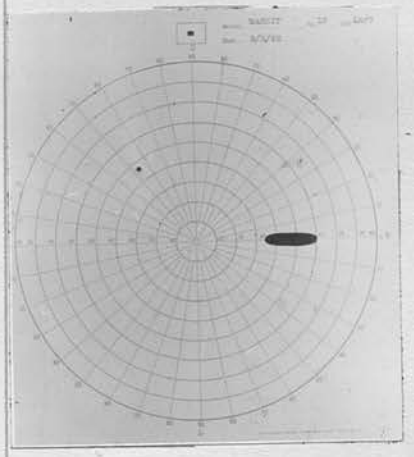


Fig. 37

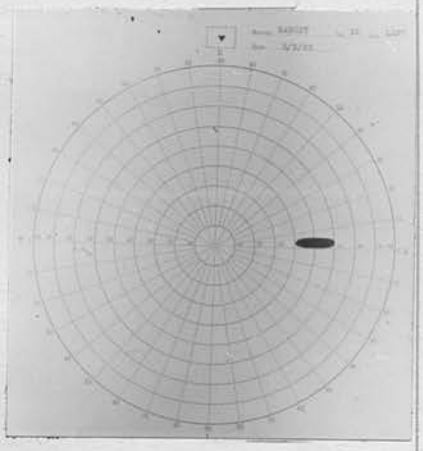


Fig. 38

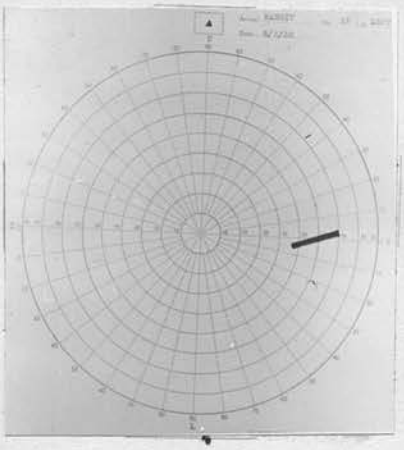


Fig. 39

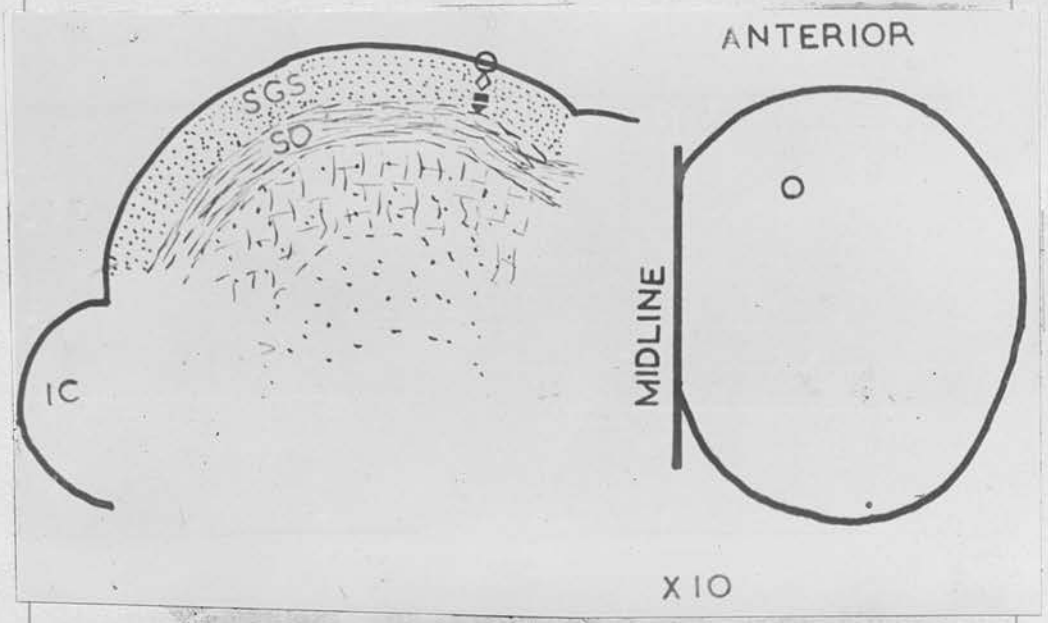


Fig. 40 shows where response was obtsined from in one stab in superior colliculus of rabbit (corresponds to No. 6 in the tables). The areas in the field of vision are in the following charts. Figs. 41,42,43,44.

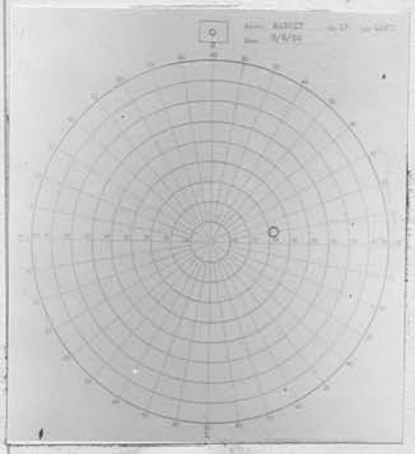


Fig. 41

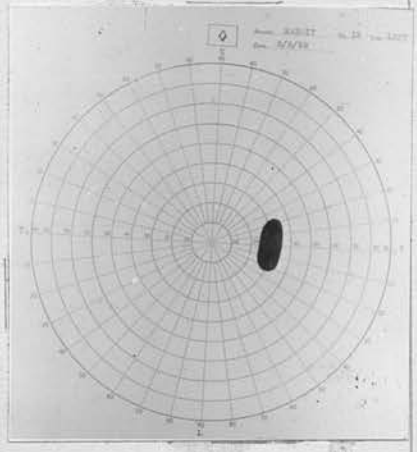


Fig. 42

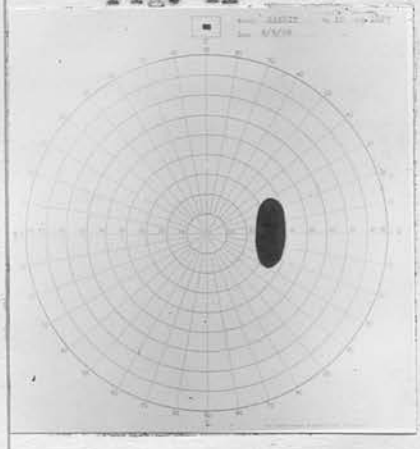


Fig. 43

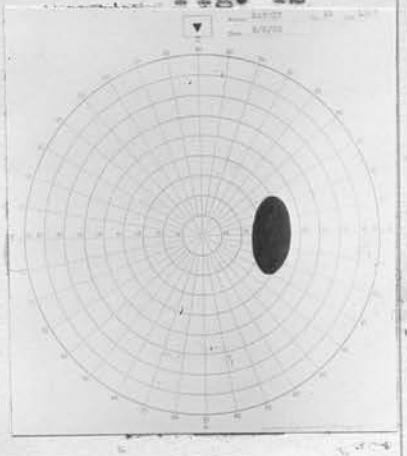


Fig. 44

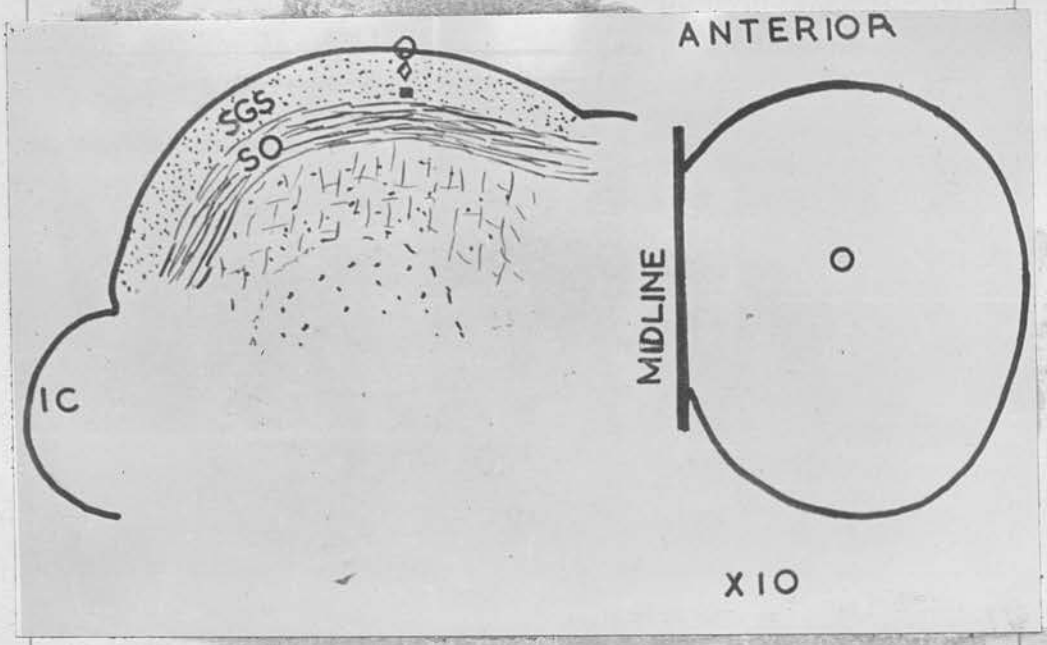


Fig. 45 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 7 in the tables). The areas in the field of vision are in the following charts. Figs. 46, 47, 48.

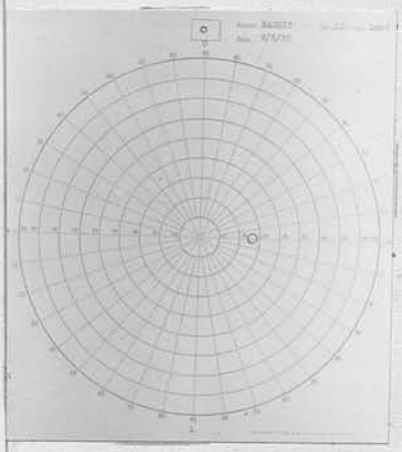


Fig. 46

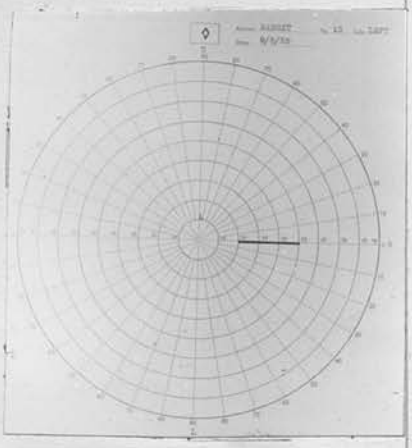
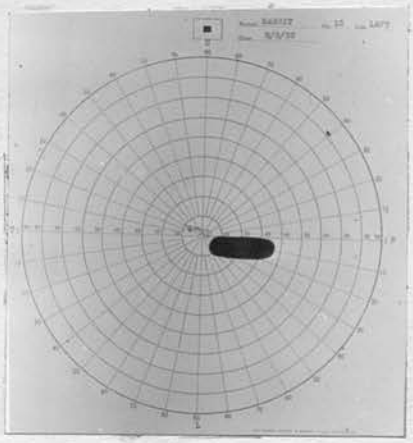


Fig. 47



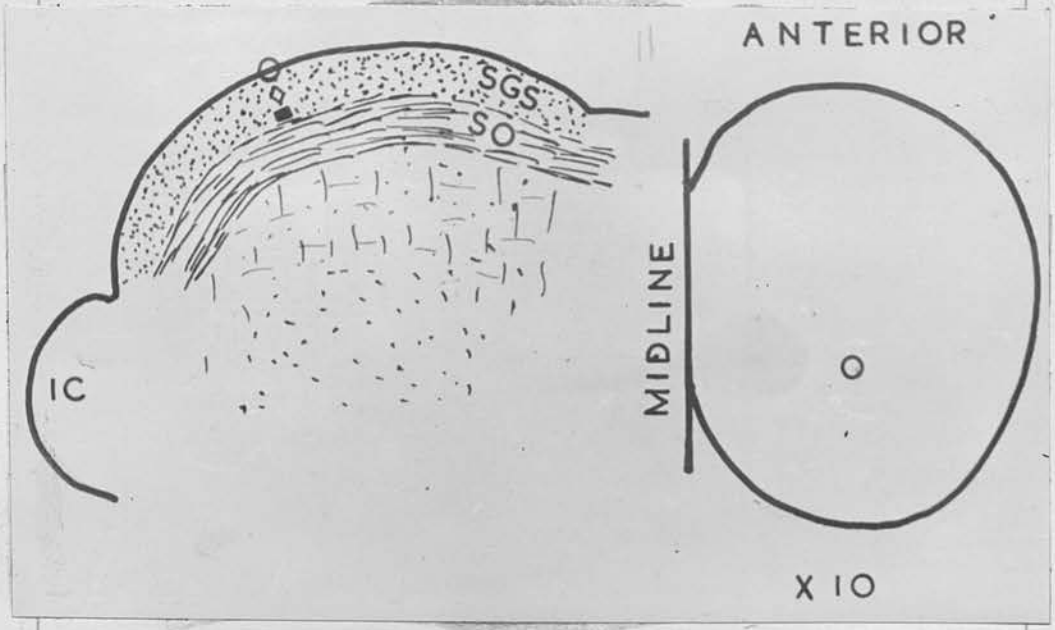


Fig. 49 shows where response was obtained from in one stab in superior colliculus of rabbit (corresponds to No. 11 in the tables). The areas in the field of vision are in the following charts. Figs. 50, 51, 52.

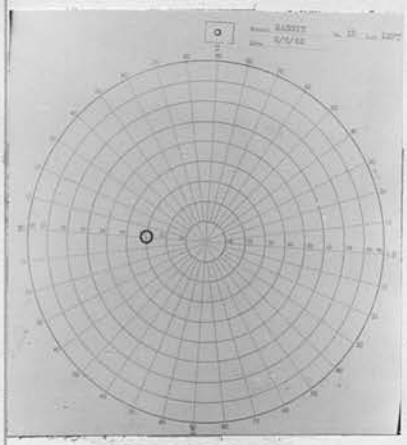


Fig. 50

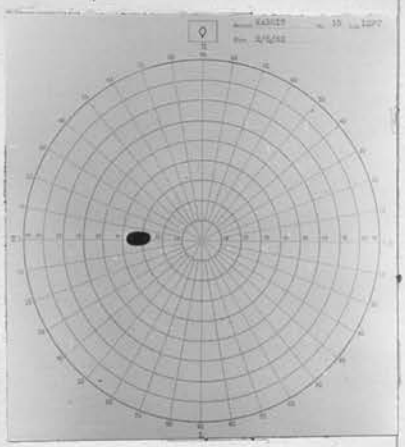


Fig. 51

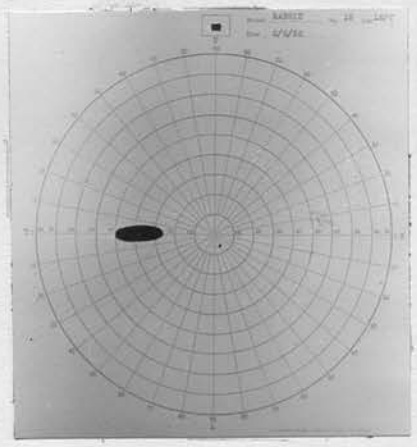


Fig. 52

Goat

Nine preparations were made. One only was disappointing (Goat 8). For some unknown reason neither the colliculus nor the visual cortex gave a satisfactory response.

Altogether thirty-nine stabs were made for the colliculus and forty-five for the cortex. The surface mapping was again an easy task and in fact in the later experiments when an idea was formed about the mapping it was possible to insert the needle in a certain part of the colliculus and put the stimulus in the part of the field which according to the measurements should give a response. This never failed.

Out of the thirty-nine stabs intended for the colliculus, six were disregarded in the results. Eleven only reached the surface or failed to give any response when put deep in the colliculus. Twenty stabs were successfully studied throughout the depths of the colliculus. Again as in the rabbit the response obtained when the needle was on the surface was quite localized, but got wider as the needle was driven into the deeper layers. The patterns mapped in the visual field when the needle was deep were a little different from what was obtained in the rabbit for example no sharp thin arcs concentric with the fixation point were

obtained. The results are tabulated and diagrams of the histological sections showing the points from which the responses were obtained are shown.

As in the rabbit it was found that the lower half of the visual field is projected on the medial half of the superior colliculus, the upper half of the visual field is projected on the lateral half of the superior colliculus. The temporal half of the retina or the nasal half of the visual field is projected anteriorly on the colliculus while the nasal half of the retina or temporal half of the visual field is projected caudally on the colliculus (Fig. 53).

Again the central visual field occupies a much wider area on the surface of the colliculus than the peripheral field (Figs. 54, 55)
As reference to fixation point the optic axis was used. (The pupil of the goat is elongated and the long axis lies horizontally).

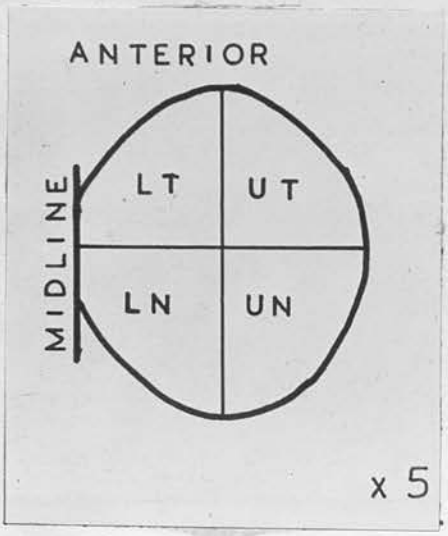


Fig. 53 shows the projection of the different quadrants of the left retina on the right superior colliculus of the goat.

LT: lower temporal
UT: upper temporal
LN: lower nasal
UN: upper nasal

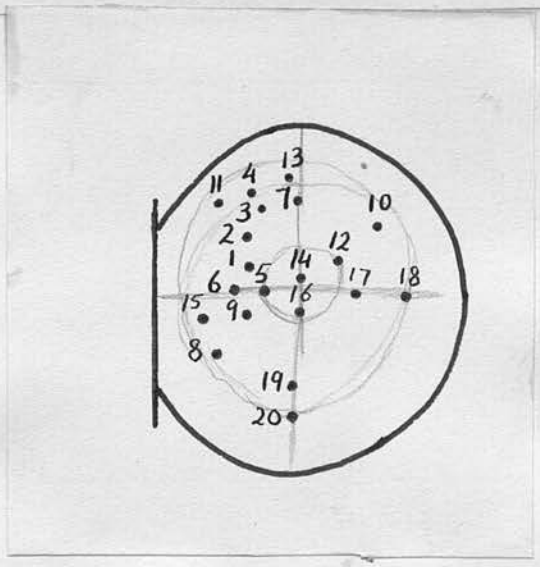


Fig. 54. Diagram of right superior colliculus of goat looked at from above, showing positions of needles (from different animals). The corresponding points in the visual field are shown in Fig. 55.

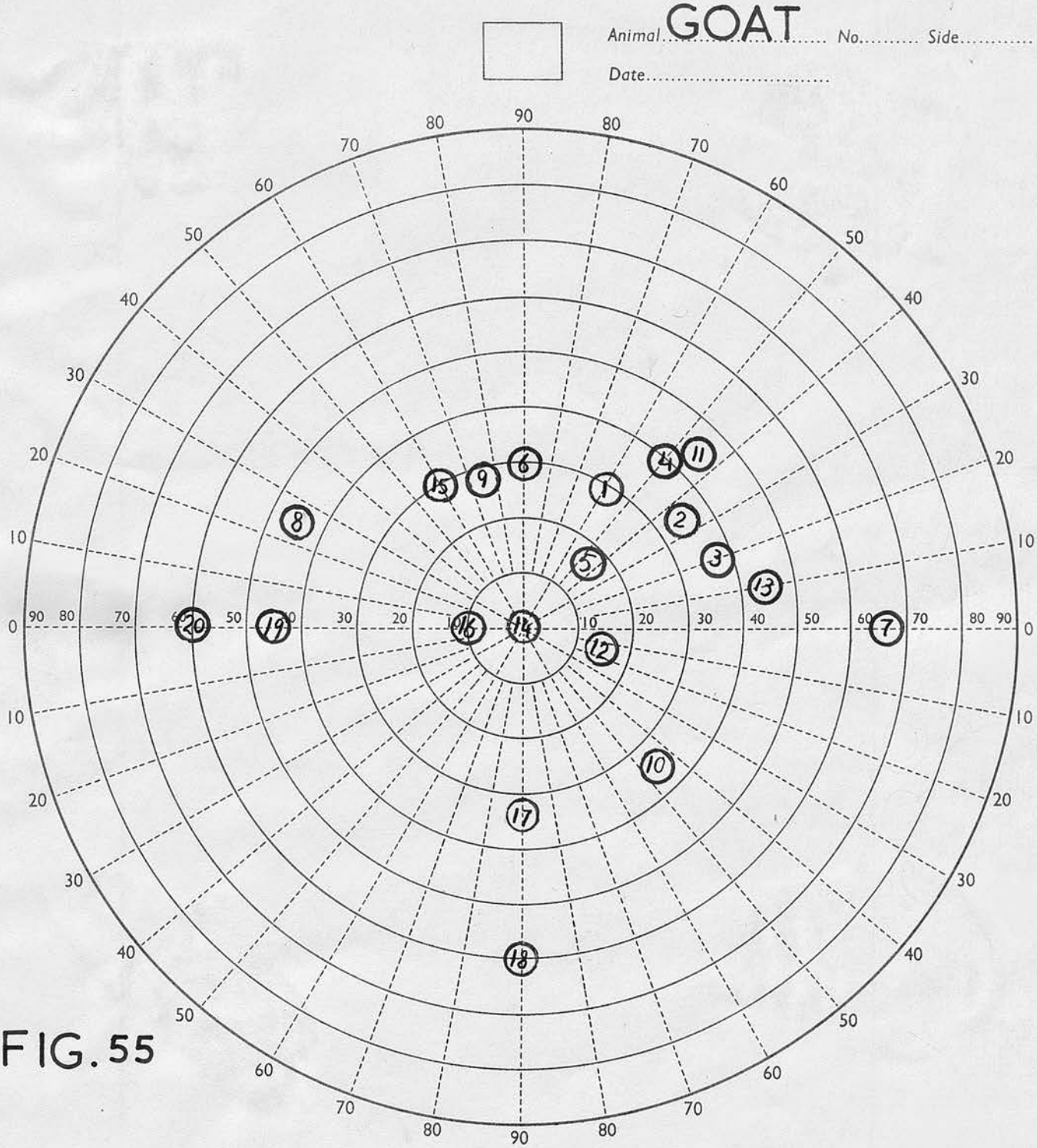


FIG. 55

Fig. 56 has been omitted.

No.	G.	Anaesth.	Response from S.Z.	Response from SG.S.	Response from S. O.	Response from deeper layers
1	1	Nembutal Ether	localized	compound figure & oblong patch "collicular" alpha rhythm for a short time	short thick arc	faint visual response. Response obtained from mes-encephalic root of 5th N. on moving the jaw
2	1	Nembutal Ether	localized	remained localized B.P. was very low & polarity of spikes was reversed	faint	none
3	2	Urethane chloralose	localized	thin arc	faint	none
4	2	ditto	localized at fixation point	remained localized	none	none
5	2	ditto	localized	thick arc	none	none
6	2	ditto	localized	thick arcs	thick arcs & compound figures	none
7	2	ditto	localized	thick arc	localized	none
8	2	ditto	localized	thick arc	faint	none
9	3	ditto	localized	oblong patch and sector	oblong patch and sector	none
10	3	ditto	localized	localized	oblong band	none
11	5	ditto	localized	short thick arc	short thick arc	none
12	5	ditto	localized	oblong patch	compound figure & oblong patch	none

No.	G.	Anaesth.	Response from S.Z.	Response from S.G.S	Response from S.O.	Response from deeper layers
13	5	Urethane chloralose	localized	thick arc and compound figure	compound figure	faint
14	5	ditto	localized	sectors	sectors and thick arcs	faint
15	5	ditto	localized	thick arc	none	none
16	5	ditto	localized	oblong patch	faint	none
17	6	ditto	localized	thick arcs	faint	none
18	6	ditto	localized	compound arcs	faint	none
19	9	Nembutal	localized	round patch	faint	none
20	9	Nembutal	localized	round patch	faint	none

G: Goat

S.Z: Stratum zonale

S.G.S: Stratum griseum superficiale

S.O: Stratum opticum

The following diagrams consist of the outlines of the sagittal sections of the superior colliculus of goats. Marks are put to show where the responses were obtained from. An open circle on the surface indicates a localized response from stratum zonale. The point of entrance of the needle is shown as a circle on the outline of the superior colliculus. This is followed by charts of the visual field showing where the response came from. Each chart has a mark at the top which is identical with the one on the sagittal section where the response was obtained.

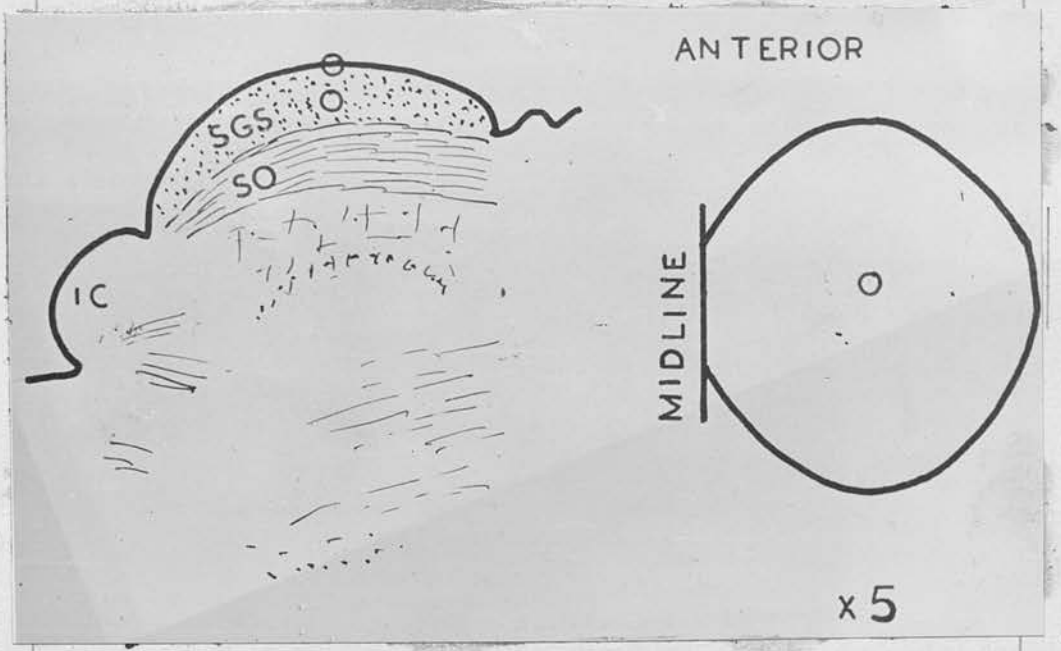


Fig. 57 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 2 in the tables). The area in the field of vision is shown in the following chart F.g 58.

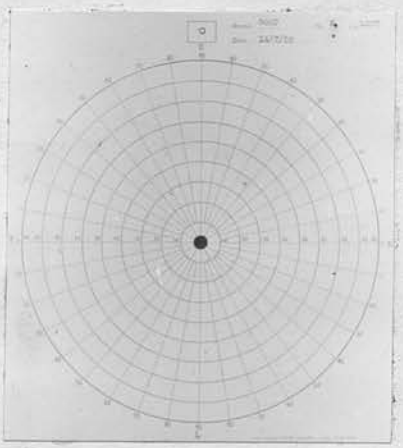


Fig. 58

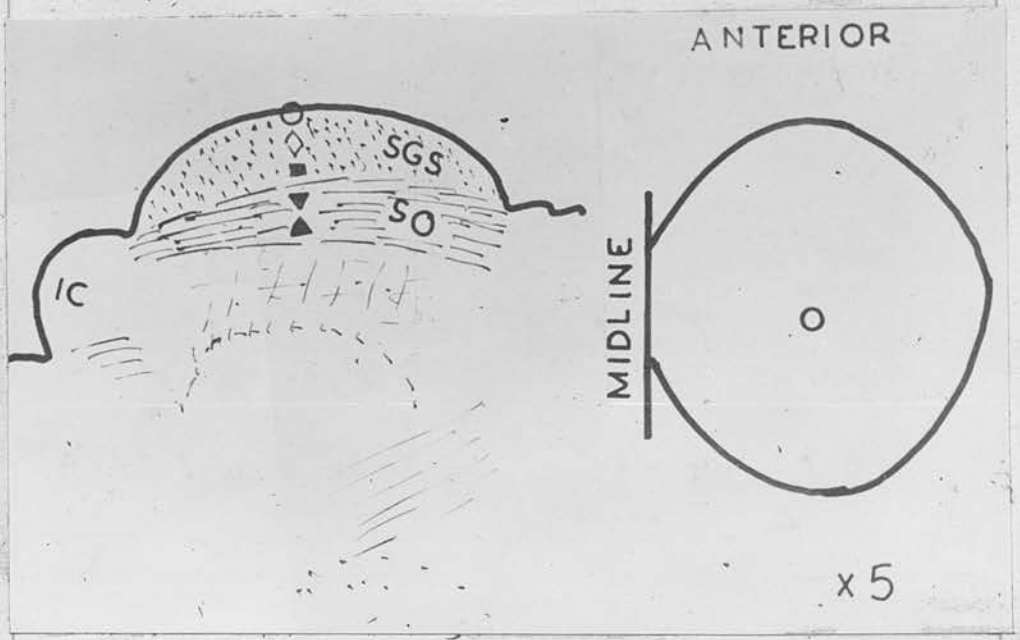


Fig. 59 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 9 in the tables). The areas in the field of vision are shown in the following charts. Figs. 60, 61. 62, 63, 64.

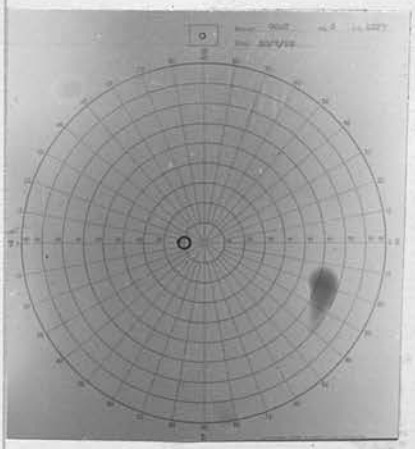


Fig. 60

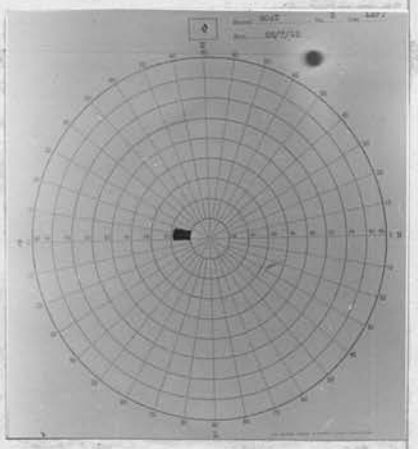


Fig. 61

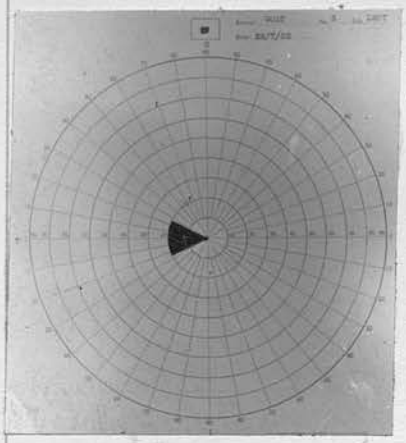


Fig. 62

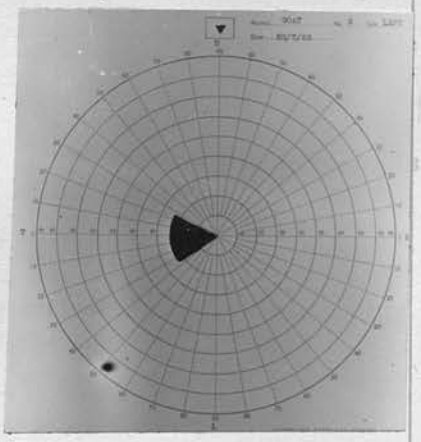


Fig. 63

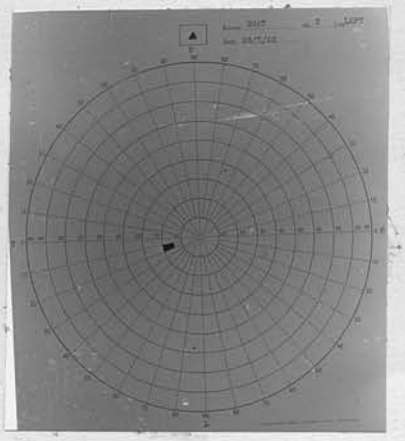


Fig. 64

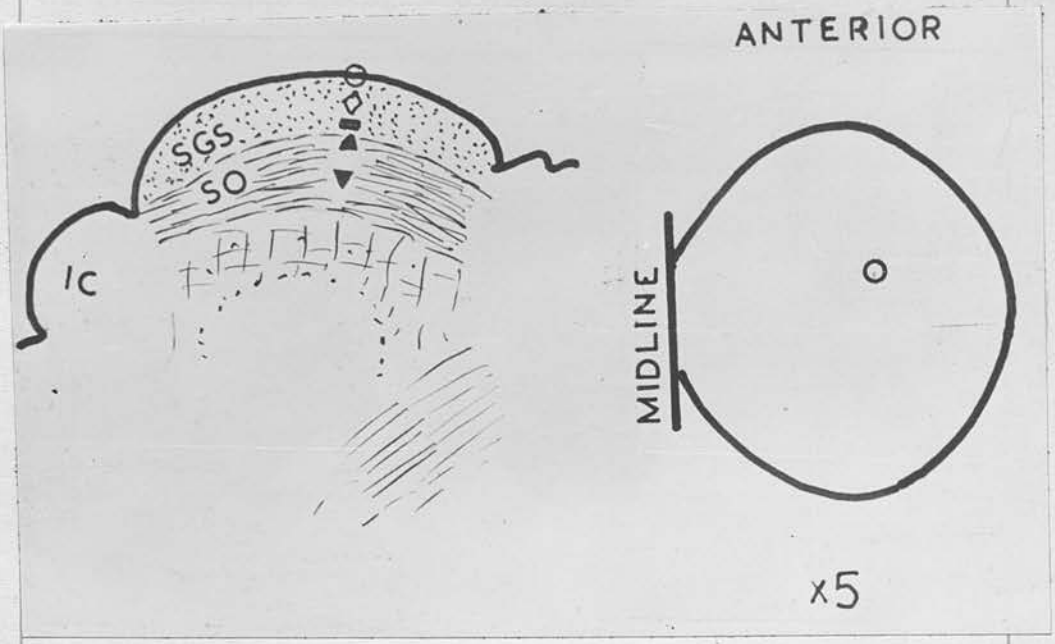


Fig. 65 shows where response was obtained from in one stab in the superior colliculus of gost (corresponding to No. 14 in the tables). The areas in the field of vision are shown in the following charts. Figs. 66, 67, 68, 69, 70.

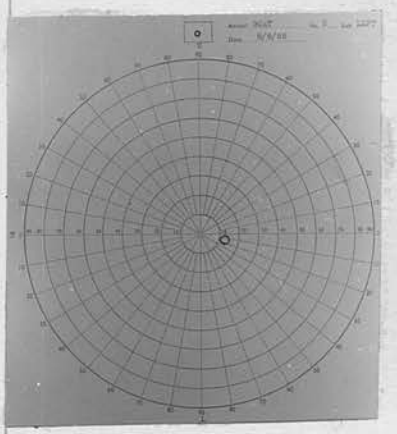


Fig. 66

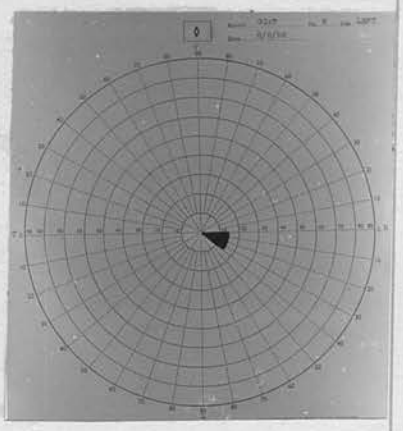


Fig. 67

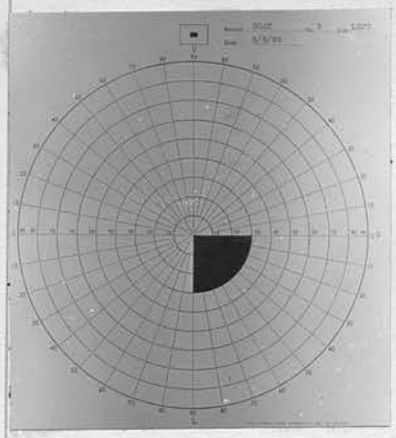


Fig. 68

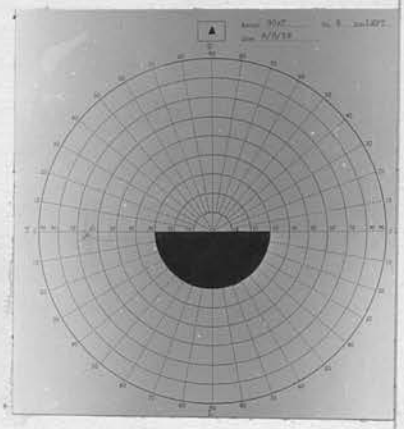


Fig. 69

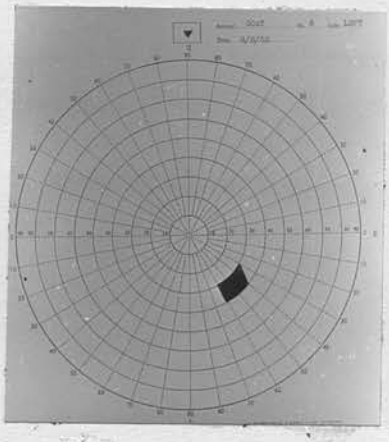


Fig. 70

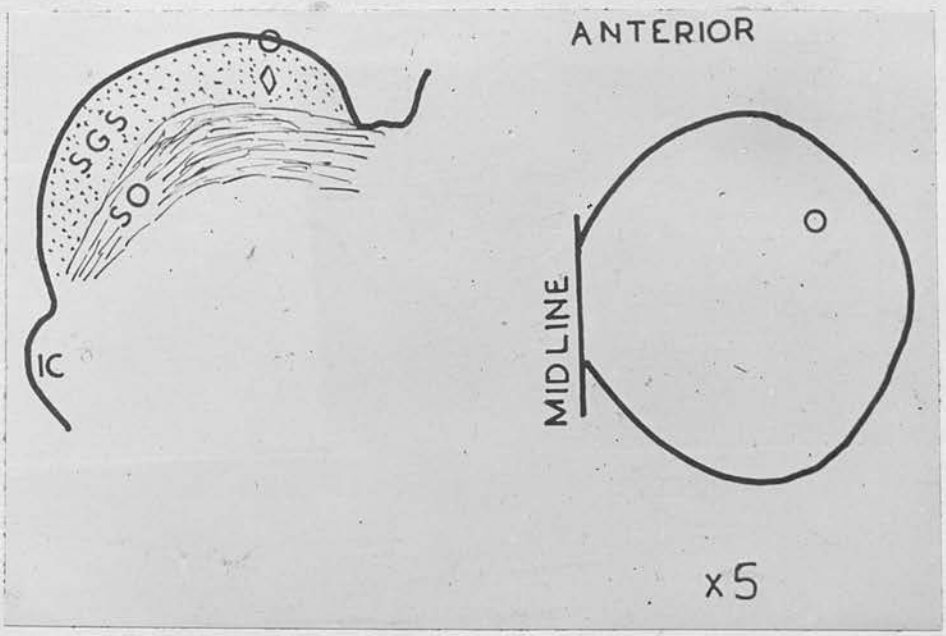


Fig. 71 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 15 in the tables). The areas in the field of vision are shown in the following charts. Figs. 72, 73.

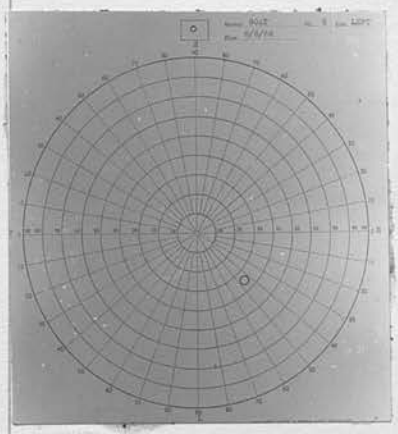


Fig. 72

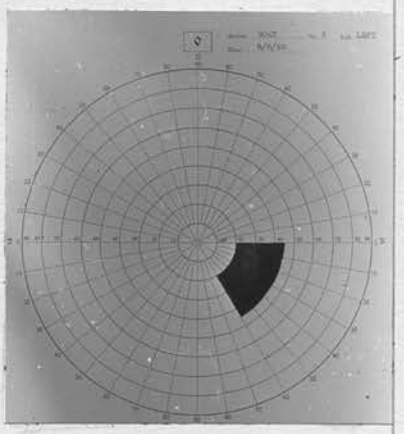


Fig. 73

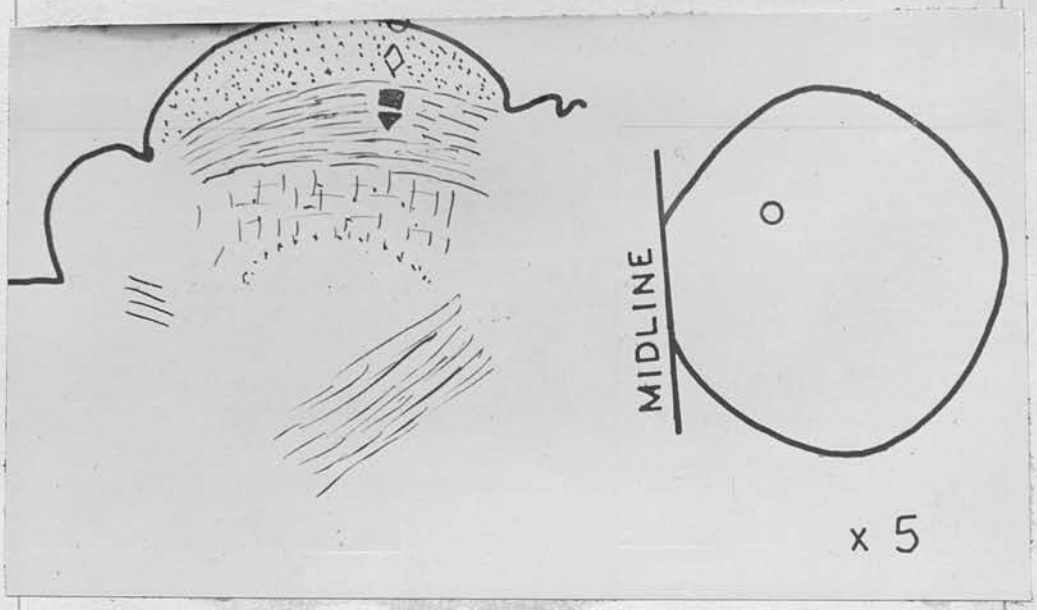


Fig. 74 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 12 in the tables). The areas in the field of vision are shown in the following charts. Figs. 75, 76, 77, 78.

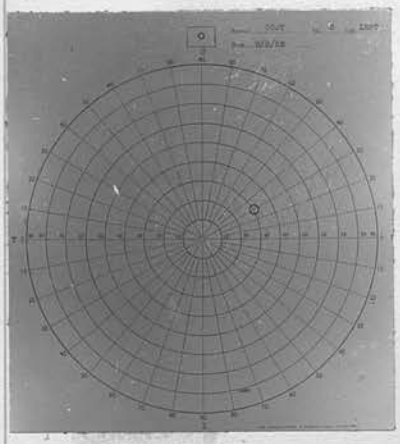


Fig. 75

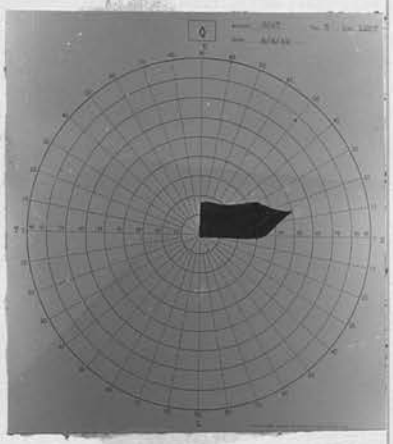


Fig. 76

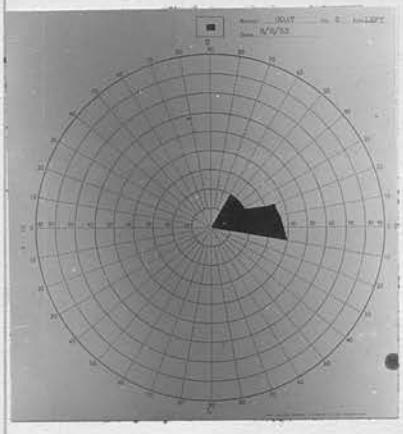


Fig. 77

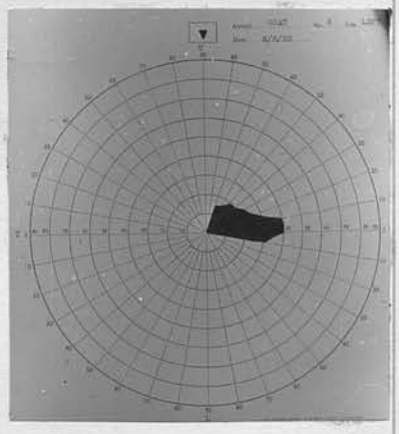


Fig. 78

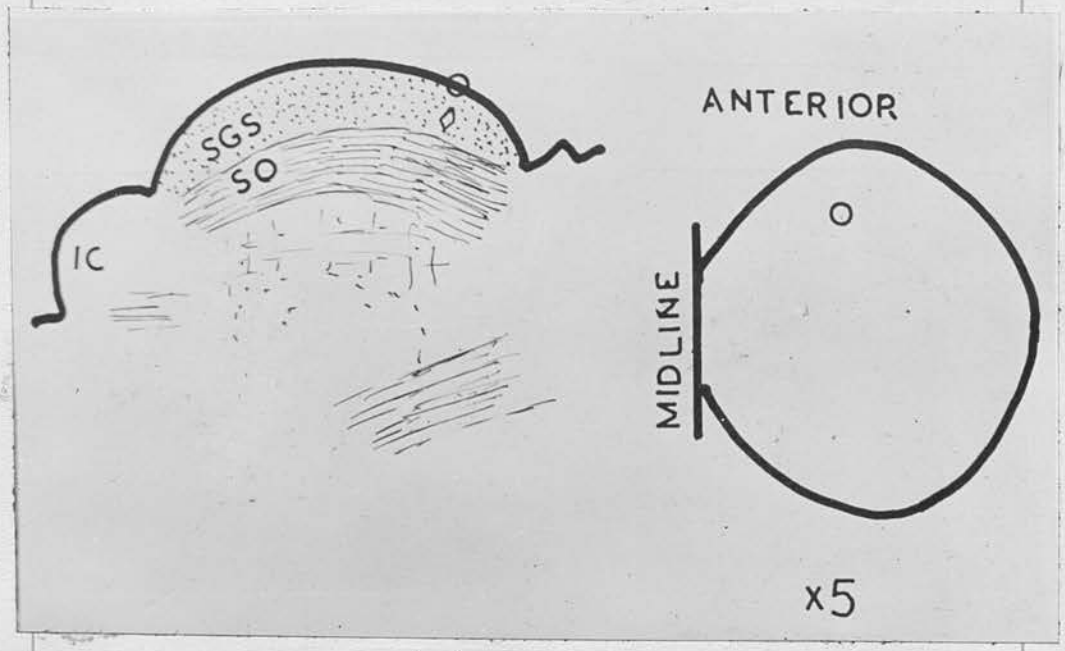


Fig. 79 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 16 in the tables). The areas in the field of vision are shown in the following charts. Figs. 80, 81.

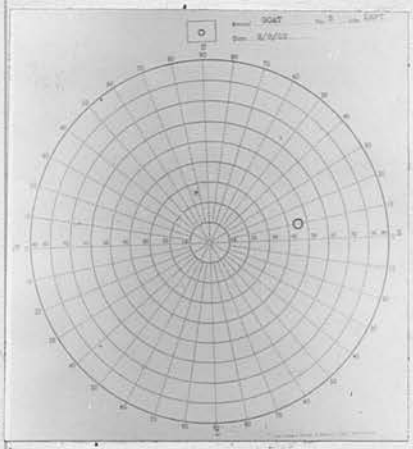


Fig. 80

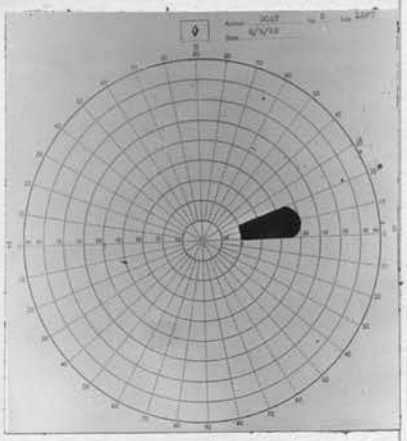


Fig. 81

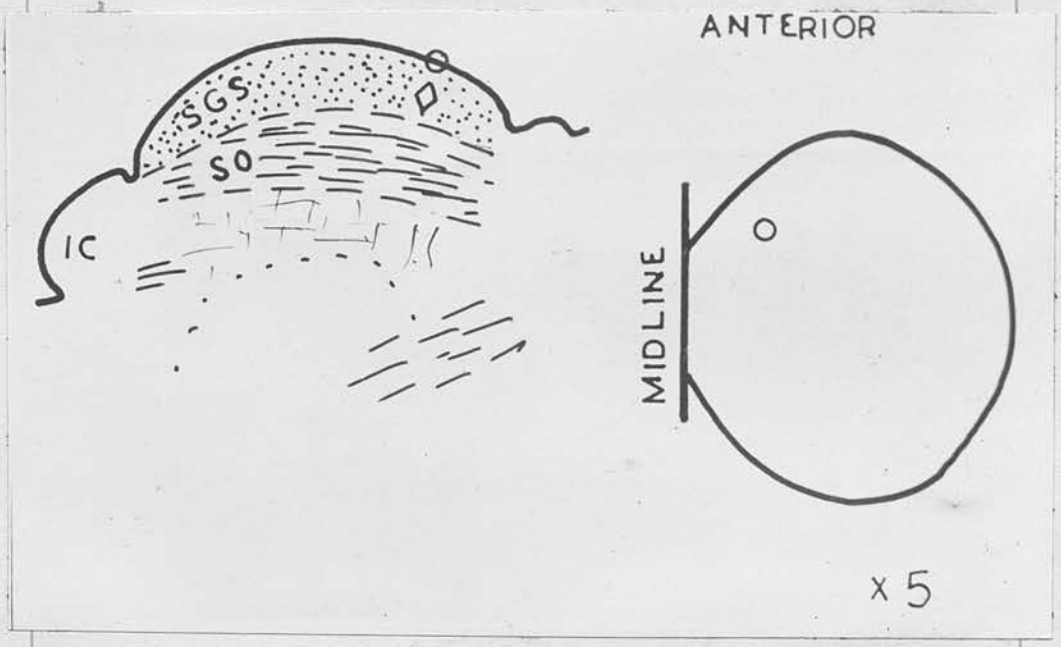


Fig. 82 shows where response was obtained from in one stab in the superior colliculus of goat (corresponding to No. 18 in the tables). The areas in the field of vision are shown in the following charts. Figs. 83, 84.

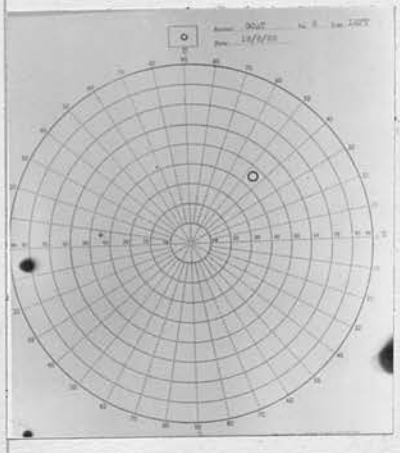


Fig. 83

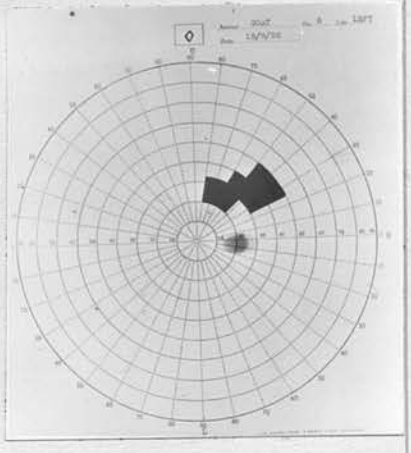


Fig. 84

Pigeon

Ten preparations were made. Three died from anaesthesia (two from chloral hydrate and one from ether). Of the seven successes, three were decerebrated on the right side and four decerebrated on both sides. The insertion of needles was actually easy because the optic tectum was under direct vision.

Point to point localization of the retina on the surface of optic tectum was obtained. No patterns were obtained from the visual field when the needle was deeper than the surface as was obtained in the rabbit and goat. At most a wider area (of about 5^{o} in diameter) from some depths of the optic tectum was observed but these were occasional.

The optic tectum of the pigeon as in other birds differs considerably in shape from the familiar appearance of the superior colliculus in mammals. It has an upper flat surface surrounded by an illdefined edge on the anterior, lateral and posterior margins. From this edge one can follow an anterior surface, and an enormous lateral surface which is continuous with the under surface. So the optic tectum looks more or less like a boat.

Most of the needle stabs were carried down (after recording from the upper surface) through the substance of the optic tectum to reach the under surface; thus one needle stab would explore the

upper surface, the deeper layers and the otherwise inaccessible under surface. (Figs. 85 & 86).

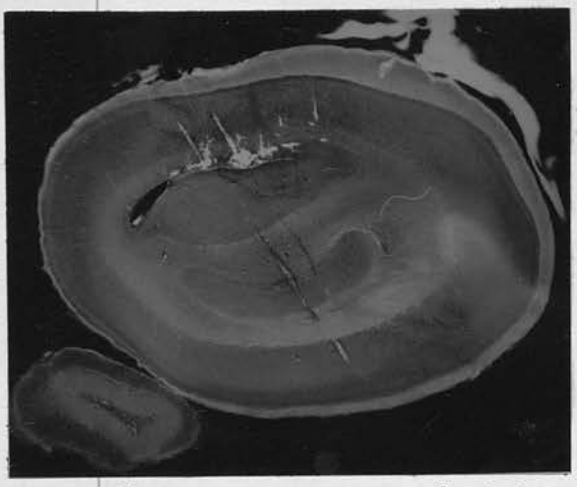


Fig. 85

Fig. 86

Figs. 85 and 86 two examples of sections cut through optic tectum of pigeon to show needle tracks reaching the under surface of the tectum.

An example from two pigeons (5 and 6) is given in Fig. 87 accompanied by a chart of the visual field responses Fig. 88. Stabs (2, 3, 4, 5, 6, 7, 8, 9, 10, 11) show the mapping of retina on the superior surface only. Stabs (1, 12, 13, 14) show the mapping on both the superior and the inferior surfaces.

The upper nasal quadrant of the visual field or the lower temporal quadrant of the retina is projected on the anterior half of the upper surface of the optic tectum. The upper temporal quadrant of the visual field or the inferior nasal quadrant of the retina is projected on the caudal half of the upper surface of the optic tectum. The lateral edge represents

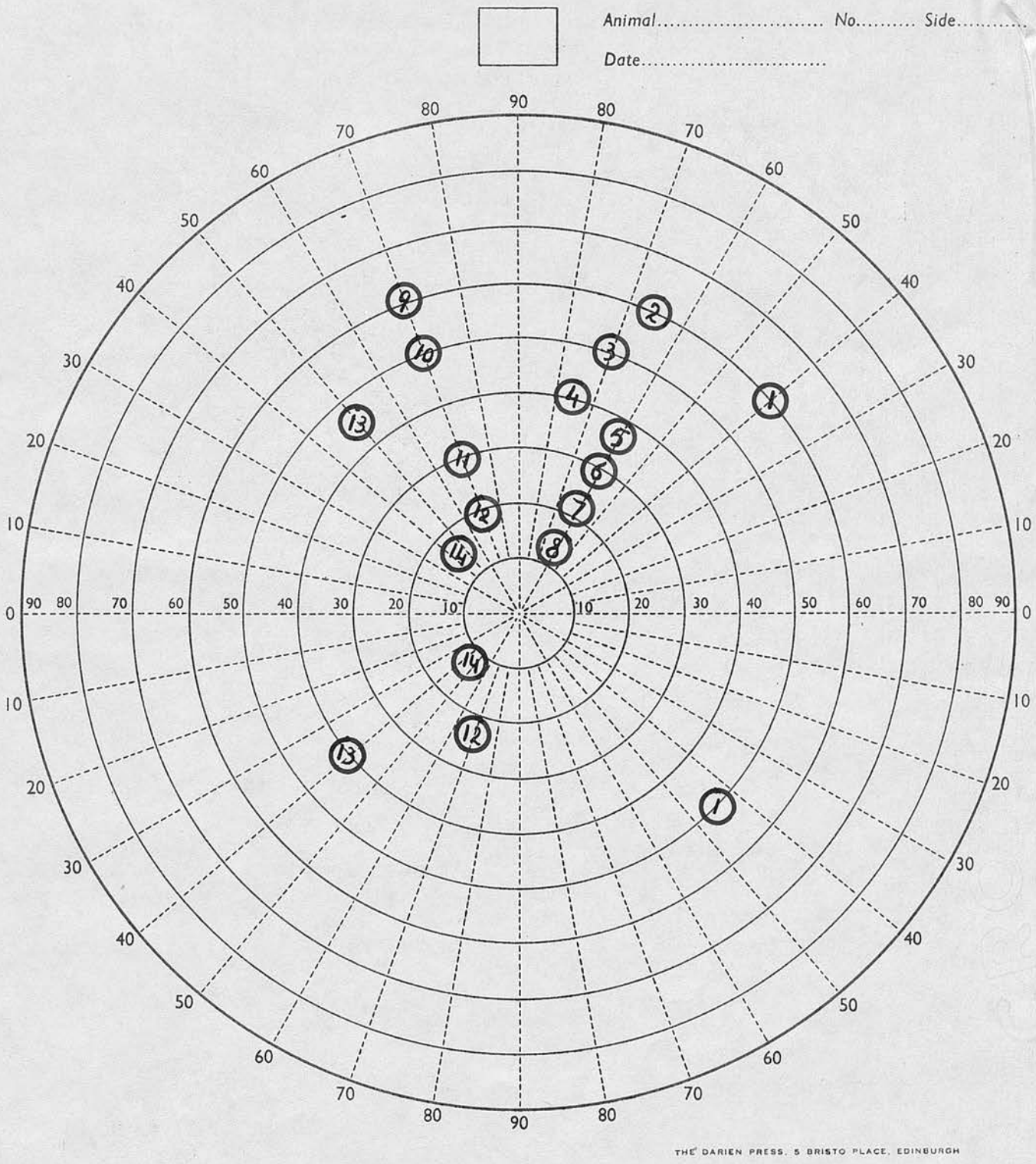


Fig. 88

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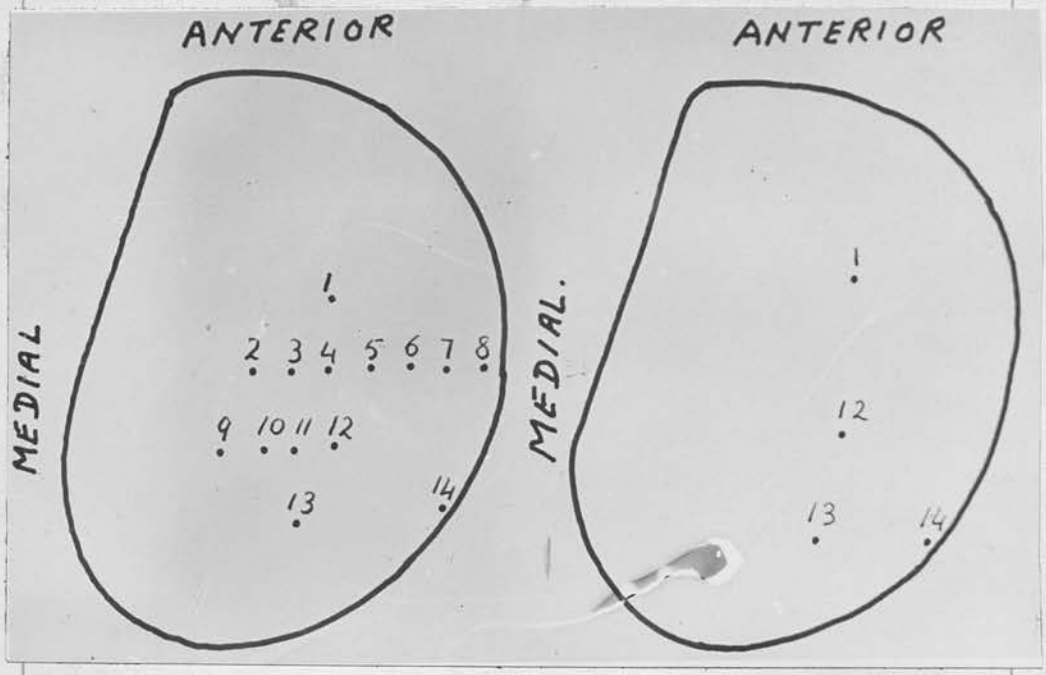


87a 87b

Fig. 87 Right optic tectum of pigeon, 87a represents the upper surface, 87b represents both the lateral and under surface as if looked at from above. 1 to 14 on 87a show points on surface where needle touched and then pierced the optic tectum. 1, 12, 13, and 14 in 87b show points on the lateral and under surfaces where the corresponding ones in 87a are the sites of entrance of needles. The visual chart is shown in Fig. 88.

halves of the visual field. The lower nasal quadrant of the visual field or the upper temporal quadrant of the retina is projected on the anterior halves of both the lateral and under surfaces of the optic tectum. The lower temporal quadrant of the visual field or the upper nasal quadrant of the retina is projected on the posterior halves of the lateral and under surface of the optic tectum (Fig. 89).

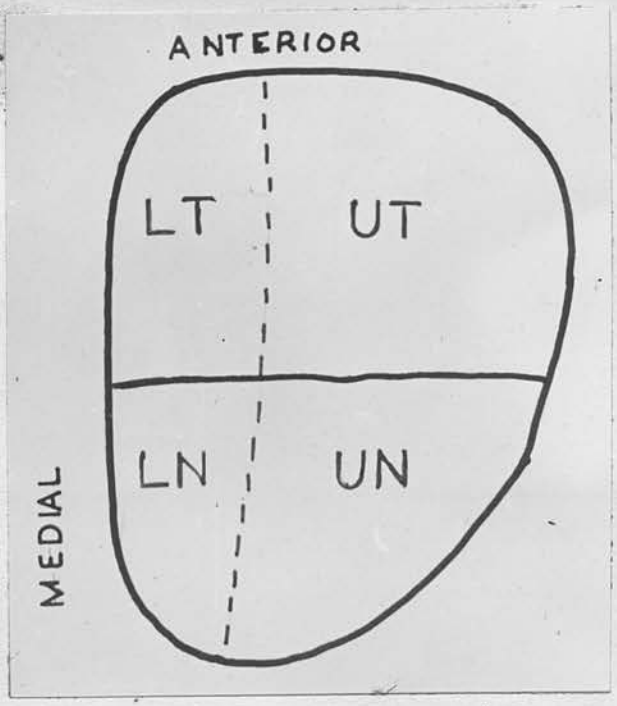
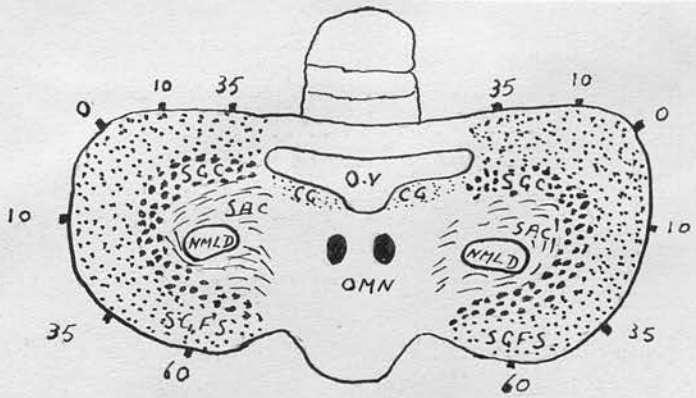


Fig. 89 The right optic tectum of pigeon as looked at from the side. The dotted line represents the lateral edge. The projection of the retina is shown.

L.T.: lower temporal quadrant on anterior half of superior surface
L.N.: lower nasal quadrant on posterior half of superior surface
U.T.: upper temporal quadrant on anterior halves of lateral and under surfaces
U.N.: upper nasal quadrant on posterior halves of lateral and under surfaces.

The distribution of the retina or visual field on the optic tectum is not proportionate (Fig. 90). It was found that the central field occupies much more on the surface of the optic tectum than the peripheral field. The lower part of the central field especially has enormous representation on the bulging convexity of the lateral surface and compared with the anteroposterior representation in the same area, it is about five times as large as the latter.



O.V. Optic Ventricle
C.G. Central Gray
O.M.N. Oculomotor Nuclei
S.G.F.S. Stratum griseum et Fibrosum superficiale
S.G.C. Stratum griseum centrale
S.A.C. Stratum album centrale
N.M.L.D. Nucleus mesencephilicus lateralis pars dorsalis

Fig. 90. Frontal section showing both optic tecti of pigeon.
The distribution of the vertical meridian of visual field is shown in degrees.

During the journey of the needle from the upper surface to the lower surface response from visual stimulation was not obtained from all the thickness of the optic tectum. Response was obtained from the upper surface down to the roof of the ventricle. When the needle tip was in the ventricle there was complete silence. Then the needle came into the central gray, an area of cells and fibres which apparently has nothing to do with visual perception. There, in four instances it was clearly demonstrated a spontaneous discharge which was quite independent from visual stimulation, i.e. it persisted when the light stimulus was off.

Then auditory response was obtained from the inferior colliculus. This also was constant. After traversing this area visual response reappears from stimulation of the upper half of the retina i.e. from the lower half of the visual field. Figs. 91 and 92.

Fig. 91 a photograph of section through the whole thickness of optic tectum of pigeon. Fig. 92 is a diagram of the same section.

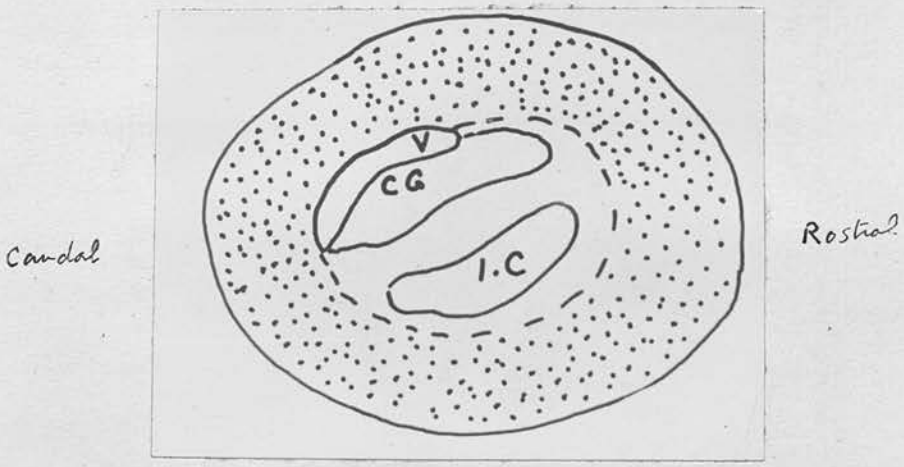


Fig. 92 diagram of the photograph of optic tectum shown in Fig. 91.

V: ventricle

C.G: central gray

I.C: inferior colliculus

The dotted area is the visual portion of the optic tectum.

HISTOLOGICAL RESULTS

The Stratum zonale in rabbit and goat could be demonstrated easily in sections stained with toluidine blue or silver stain by Roger's method (Figs. 93 and 94). It was impossible to see it in sections cut from tissue stained in block as in De Castro's method, probably due to the heavy precipitation of silver on the surface.

The stratum griseum superficiale was found to consist of small cells of about ten microns in diameter in its superficial part and larger cells of about twenty microns in the deeper part (Figs. 94, 95, 96 and 97).

The stratum opticum contains large cells of about twenty microns in diameter and similar to those in the deeper layer of the stratum griseum superficiale (Figs. 98 and 99).

The stratum lemnisci contains large cells of eighty to onehundred microns in diameter (cell body only) with very thick and long processes (Figs. 100, 101 and 102).

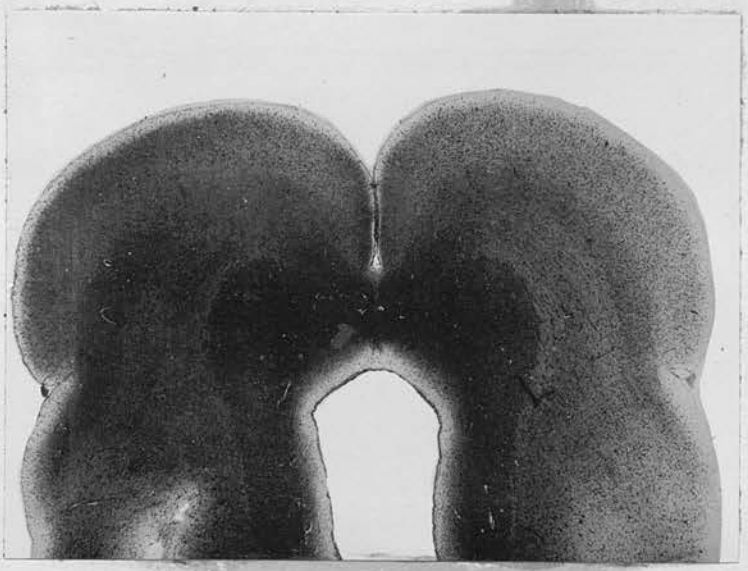


Fig. 93 frontal section in the superior colliculi of rabbit (Toluidine blue stain) showing the different cell layers. On the left the stratum zonale appears as a very thin line of cells on the surface X 11.

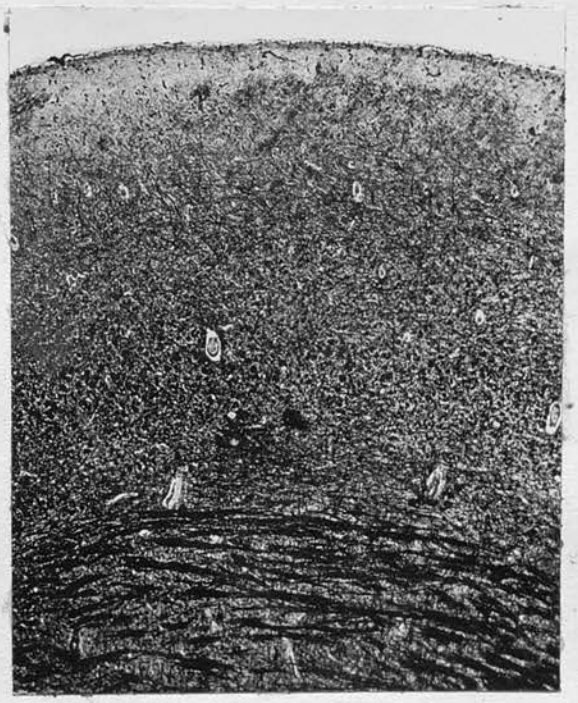


Fig. 94 sagittal section in superior colliculus of rabbit (Roger's silver stain) showing the stratum zonale and some of the cells of the stratum griseum in focus. The difference in size of cells in the upper and lower parts of stratum griseum superficiale is apparent X 50

Fig. 95 From section in superior colliculus of rabbit showing the cells in deep layers of stratum griseum superficiale taking the stain lightly X 425 (Roger's silver stain).

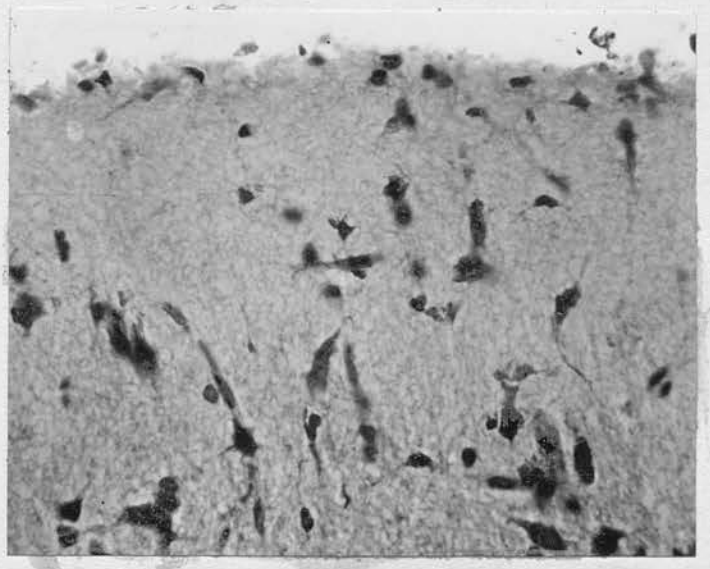


Fig. 96 Sagittal section in superior colliculus of rabbit (Toluidine blue stain) showing the small size of cells in stratum zonale and upper part of stratum griseum superficiale X 425.

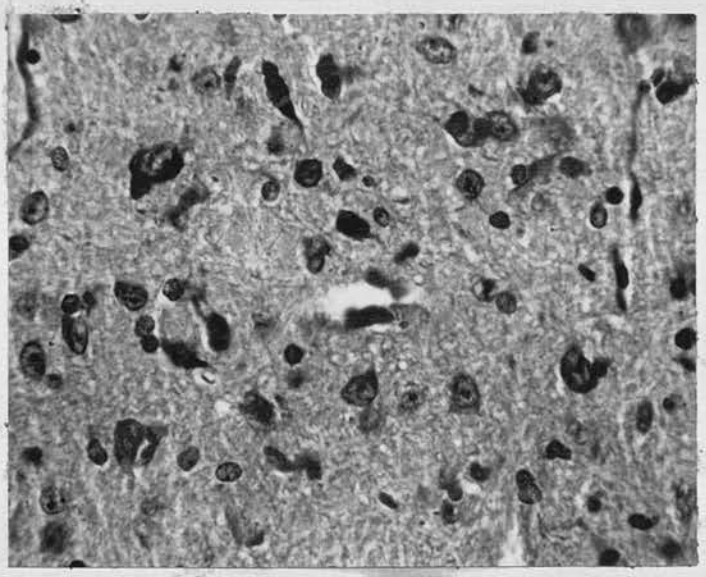


Fig. 97 From section in stratum griseum superficiale (Toluidine blue stain) showing the big cells in lower layer of this layer X 425 compare with the following Fig. which shows the cells in stratum opticum of same size.

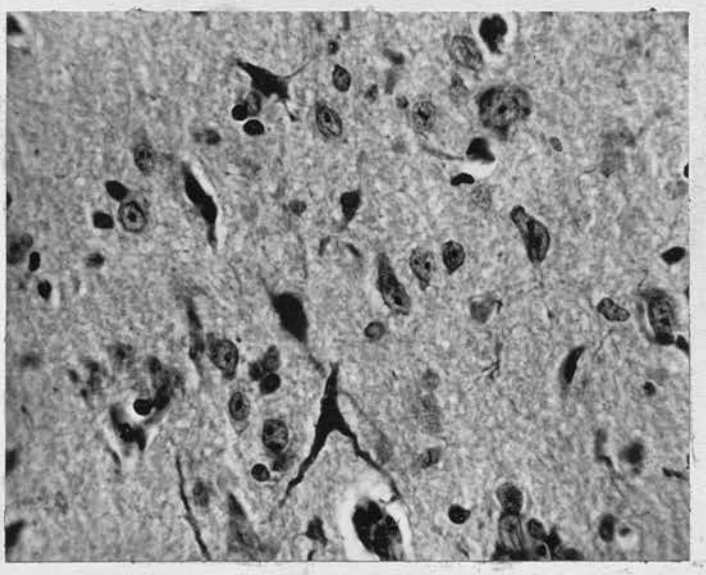


Fig. 98 Section in stratum opticum (Toluidine blue stain) showing the big cells comparable with those in deep layer of stratum griseum superficiale X 425.

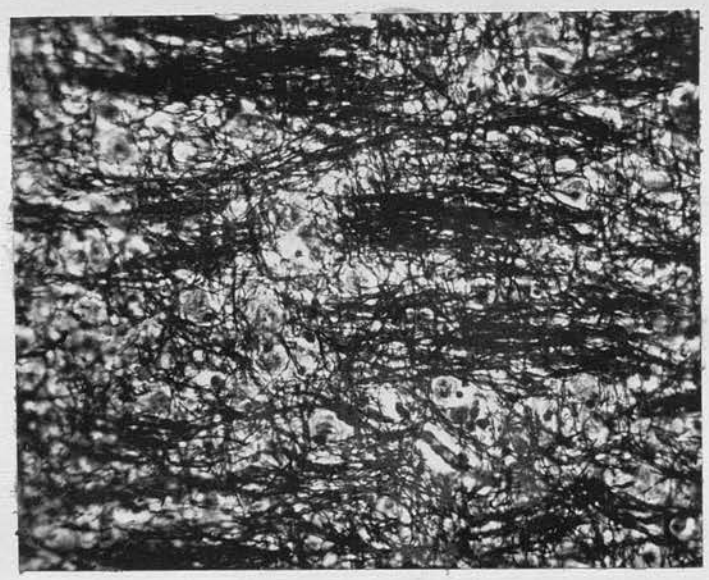


Fig. 99 Section in stratum opticum of superior colliculus of rabbit showing the fibres and of the optic tract and cells among them. Notice the abundance and big size of the cells (Roger's silver stain) X 265

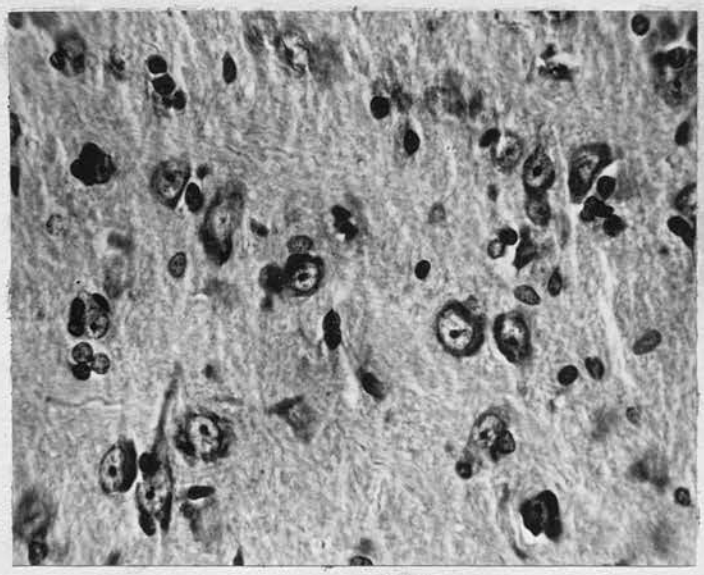


Fig.100 Section through stratum lemnisci showing the big cells (Toluidine blue stain) X 425 compare with the following two Figs.

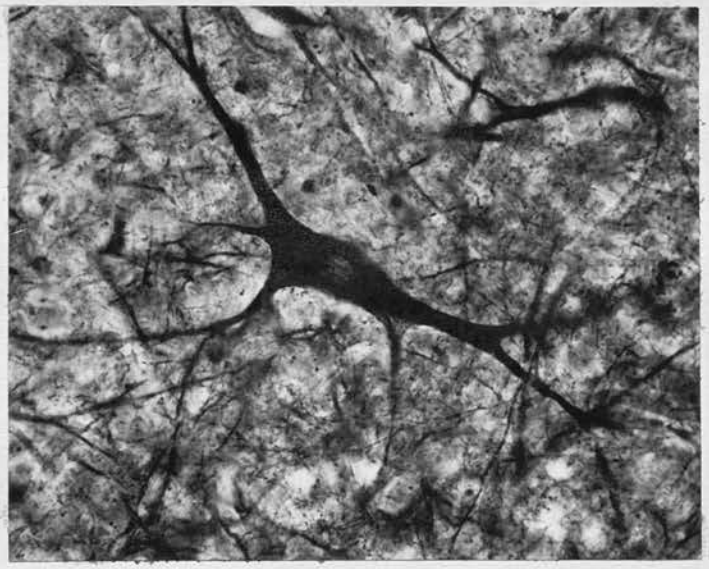


Fig. 101
X 425

Fig. 102

Figs. 101 and 102 showing cells of strstum lemnisci in superior colliculus in rabbit showing the big cells (De Castro silver) X 175

ELECTRICAL RESULTS

In rabbit and goat it was found that when the needle electrode was either on the surface of the superior colliculus or deep in the stratum griseum superficiale or stratum opticum, and a light was flashed from the corresponding point in the field of vision, electrical potentials that accompany the response to stimulation were picked up. The results were to a great extent similar in both rabbit and goat. Unfortunately no response from single units was obtained, but quite a number showed spikes instead of slow waves.

The latent period: in this case between the flashing of light stimulus and the appearance of the response was 30 msecs. (Figs. 103, 104, and 107).

However there was another response to the same stimulus which always appeared later than this. (Fig 103)

It is interesting to note that when the needle was deeper than the surface of the superior colliculus and a response was obtained from a wider area in the field and especially if it were of a large diameter, the response with shorter latency always occupied a smaller area in the field, and was always in the centre of the area of response, whereas the response with longer latency could be obtained from all over the area of response in the field. In one instance (rabbit 16) the area giving the response with shorter latency was occupying a sharp point whereas the area of response with a longer latency was

occupying a wide area. This was the feature when the tip of the needle electrode was in the superficial layer of the stratum griseum superficiale, but when the tip of the electrode reached the deeper layer of the same stratum, the response with the short latency disappeared completely and the one with the longer latency persisted.

In one rabbit and in one goat a spontaneous discharge at a frequency of 30-40 impulses/sec. was noticed in the dark and was inhibited at flashing the light stimulus "collicular alpha rhythm" (Figlos) There was no localization of the inhibition i.e. it occured wherever the light stimulus was in the field of vision.

As regards facilitation effect by a second stimulus, it was found that when the second stimulus was located within 10^{o} on the perimeter away from the first stimulus, and both are within an area in the field giving response, and provided the two stimuli were simultaneous then facilitation occured. When on the other hand they were not simultaneous, inhibition occured. This inhibition occured even when the two stimuli were separated by a distance up to 25^{o} on the perimeter, whether vertically or horizontally. At this distance of separation and the two stimuli being simultaneous, no facilitation was observed.

As facilitation, inhibition also occured only when the two stimuli were in the area of the field

which gave response.

The most marked and constant facilitation, however, was obtained when the two stimuli were close together, and not more than 2° apart.

In one goat (goat 3) while the needle tip was in the deeper layers of the stratum griseum superficiale, a response was obtained by putting the usual stimulus (1mm in diameter) which subtends an angle of 0.55° on the perimeter. This response as usual consisted of an early and a late component. When a diffuse light was flashed in front of the eye the late component disappeared and the early persisted. This was repeated several times and was found constant.

In the pigeon, it was also noticed that the response was of two components, the faster one was of 22 msecs. latency while the late one was 50 msecs. The wider areas in the field obtained when the needle electrode was in the stratum griseum superficiale which were obtained in rabbit and goat and had characteristic shapes were not obtained in the pigeon, instead only a widening of the area of response could be noticed in some cases. This also had the characteristic two components of the response. (Figs 108, 109 & 110)

In the pigeon and rabbit there was rapid adaptation of the long latency response to the light stimulus.

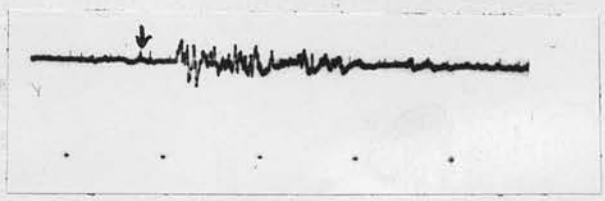


Fig. 103 Response from stratum griseum superficiale of superior colliculus of rabbit in response to light stimulus. Time $\frac{1}{10}$ sec.

Arrow : light stimulus.

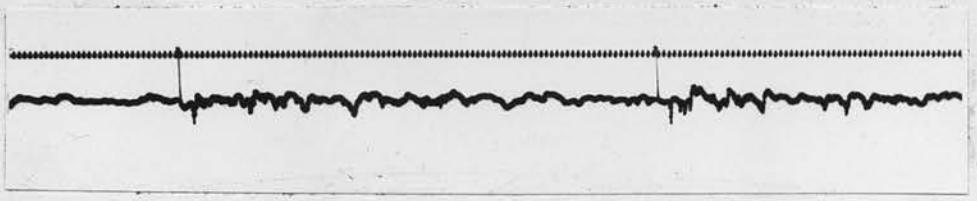


Fig. 104 Response from superficiale layers of stratum griseum superficiale of superior colliculus of rabbit in response to light stimulus. Time $\frac{1}{100}$ sec.

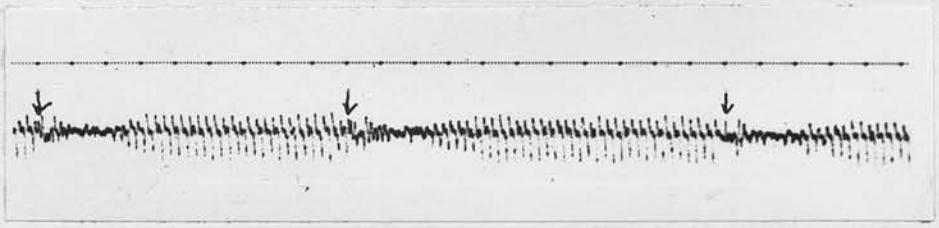


Fig. 105 Discharge obtained from stratum griseum superficiale of superior colliculus of rabbit showing "colliculus alpha rhythm" and the inhibition obtained when the light stimulus was switched on. Frequency 40/sec.

Time $\frac{1}{10}$ sec

Arrows point to light stimulus.

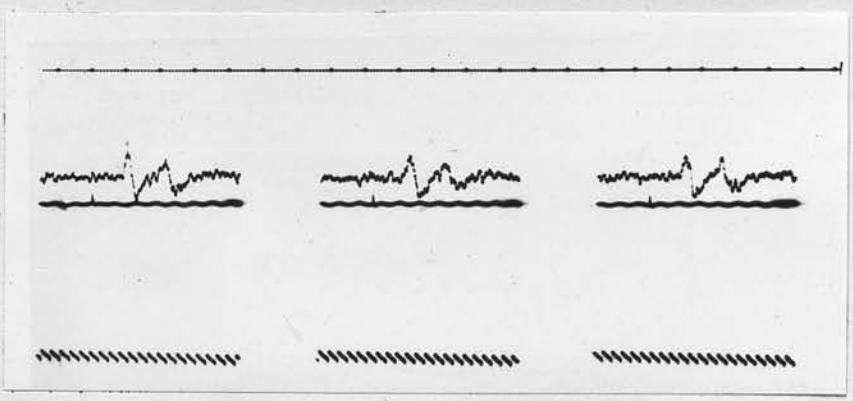


Fig. 106 Responses from stratum griseum superficiale in superior colliculus of goat in response to light stimulus. Time $\frac{1}{10}$ sec.

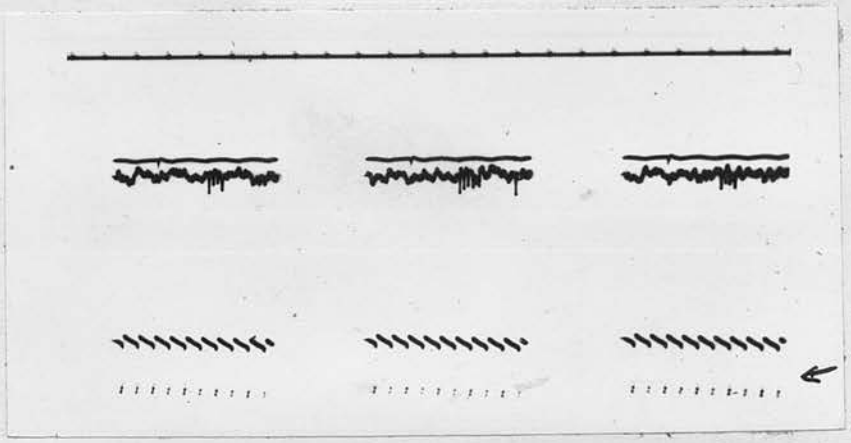


Fig. 107 Spike potentials from superficial layers of stratum griseum superficiale of goat in response to light stimulus. Time $\frac{1}{100}$ sec.

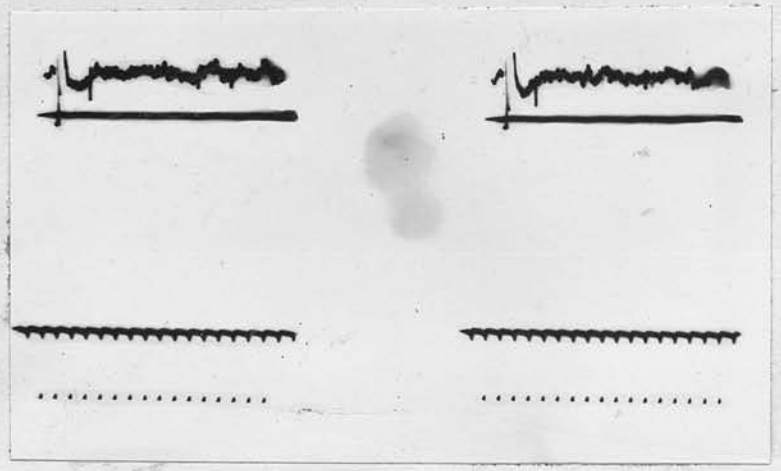


Fig. 108 Early response (spike potentials) from optic tectum of pigeon to light stimulus. Time $\frac{1}{100}$ sec.

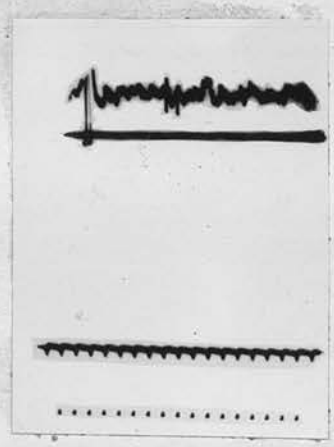


Fig. 109 Late response from optic tectum of pigeon in response to light stimulus Time $\frac{1}{100}$ sec. Latent period 55 msec.

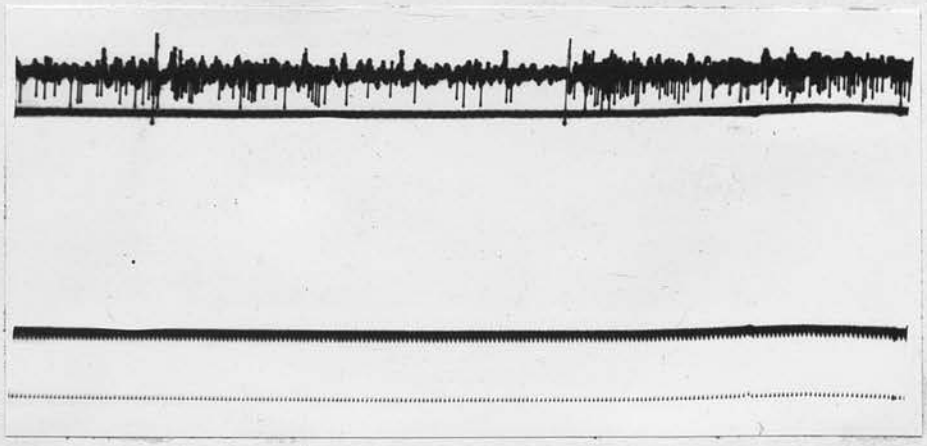


Fig. 110 Spontaneous discharges from optic tectum of pigeon and the effect of a light stimulus in increasing the frequency.

DISCUSSION

The potentials picked up from the surface of the superior colliculus in response to the light stimulus had a short latency in most cases. The potentials picked up from the stratum griseum superficiale and stratum opticum were usually composite i.e. one with a short latency followed by one with much longer latency. One would think that the first is due to impulses from the retina carried by the mesencephalic root of the optic tract directly to the superior colliculus, whereas the other with longer latency comes from the visual cortex via the cortico-mesencephalic fibres and hence the longer latency, but this is not the case because it persisted after removal of the occipital lobe, in two rabbits, most of the pigeons and in some goats where the cortex was not functioning in later hours of experiments due to prolonged exposure (as judged by absence of response when the needle was piercing the cortex on its way to the colliculus). The stimulus used in this work subtended an angle of 0.25° on the retina, and certainly it was not stimulating one receptor cell at a time, but a number of cells. Moreover, although the light stimulus is focussed by the animal's own dioptric system on its retina, to a spot maximally illuminated, yet the intra ocular reflection surrounding this spot should not be overlooked. This reflected light of course is less

bright than the direct one, but still it will stimulate optic fibres far away from the spot primarily stimulated. These fibres would carry an impulse later than that carried from the brighter spot and hence appear as longer latency. L. C. Thomson (1953) recorded spike potentials with a silver-filled glass microcapillary from single fibres of the intracranial part of the optic nerve in rabbits. The photoreceptors influencing the fibre were stimulated with a small spot of light focussed upon the retina through the normal dioptric mechanism of the eye. The receptive field of a single fibre was found to be a circular area of retina 1mm in diameter. As the stimulus spot moved towards the centre of this field the latent period between the end of the illumination and the first spike of the "off" response shortened from about eighty msecs to about five msecs, with increased number of spikes. In Thomson's experiments the area of retina contributing to the stimulation subtended an angle of about 12-15° in the visual field. If the intensity of the stimulus light was lowered thirty two times, this would make a marked difference in the measured size of the field, because reducing the intensity of the stimulus reduces the size of the aberration pattern in the image and this should be reflected in the small angle within which a response could be obtained. On the contrary

Thomson found the receptive field to be substantially similar to that recorded before the intensity of the light was reduced, so it is probably the angle subtended by the true area of reception of one nerve fibre. The geometrical size of the light spot was therefore much smaller than the area supplied by a single ganglion cell. Thomson concludes that the reduction of the latent period indicates that the large size of the field is due to interconnections between the ganglion cells and other retinal neurons.

The stratum opticum, especially the superficial half where the mesencephalic root of the optic tract ends, contains large cells of twenty microns in diameter and very similar to those in the deep layer of the stratum griseum superficiale. They are quite numerous and they correspond to the ones in the stratum griseum superficiale above them, because the localization of light stimulus in the field would not change when the needle tip reached these cells. It seems probable that the response obtained from this layer is from these cells and not from the optic fibres, because if it were from the fibres one would expect a rapid change in the localization of the light stimulus in the field as the needle goes down. The only difference noted was that these cells were less excitable than the more superficial ones in the stratum griseum

superficiale with the anaesthetics used whereas Cooper, Daniel and Whitteridge (in preparation) obtained lively responses from the stratum opticum in the goat under nembutal anaesthesia. Anyhow in this work there were quite frequently responses from this deep layer, but always fainter than the ones from the stratum griseum superficiale.

Another feature in the study of the histology of the superior colliculus is the abundance of large cells of about 80-100 microns in diameter with long processes in the stratum lemnisci and mostly situated in the caudal half of the superior colliculus. Whether the tectospinal tract originates from these cells, it has still to be investigated.

There is no doubt about the existence of the stratum zonale as an individual layer both histologically and by the fact that the termination of fibres in this zone is in such a pattern that a sharp localized response with short latency could always be obtained. This layer could never be demonstrated by silver staining in block, probably due to the heavy precipitate on the surface.

It has been mentioned before that the mapping of the retina on the superior colliculus was worked out anatomically on rabbit, rat, opossum and ferret. The results demonstrated a separate representation of the particular retinal quadrants on the superior colliculus. Brouwer and Zeeman failed to trace

macular fibres at all. Apter advanced more and could map the retina in more detail on the surface of the superior colliculus of the cat. But the projection of the minute parts of the retina in terms of point to point representation remained to be proved. Of course the word "point" in this connection does not refer to the mathematical definition which would indicate a place with no dimensions, but to describe how minute the receiving apparatus of vision is represented on such a visual centre. In this study it was proved beyond doubt that there is a point to point localization of the retina on the surface of the superior colliculus. Conditions were more complicated in the stratum griseum superficiale and the stratum opticum where certain patterns were obtained from the field of vision as seen in the diagrams. These patterns had certain features. They were either radiating from the fixation point on the perimeter or concentric with this point. Their boundaries were sharp. Whether these patterns have any importance in the reflex movements of the eyes in directing the gaze towards an object in the field is still to be proved. Anyhow Pitts and McCulloch (1947) describing neural mechanisms which exhibit recognition of forms, and using as basis for their explanations the work of Apter (1945 and 1946) of

mapping the visual field on superior colliculus of cat, they came to the conclusion that the results of Apter agree well with their hypothesis. They made use of the projection of the horizontal and vertical planes of the visual field on the superior colliculus and compared them with their hypothetical X and Y co-ordinates which they generalize and describe them even for the visual cortex. Pitts and McCulloch were trying to explain the function of the superior colliculus in directing gaze towards a certain point in the field. Although their work and conclusions are more or less theoretical yet the patterns described in the results of this study especially the straight lines and oblong patches on the horizontal plane do fit well with their theories of co-ordinates, making the colliculus to "take a weighted centre of gravity of an impingent distribution of light".

It was shown that the area centralis is represented on the superior colliculus too. It was argued that the macular fibres go to the pretectal region and not to the superior colliculus (Clark 1942) after Brouwer and Zeeman failed to follow them to the superior colliculus. Although macular fibres go to the pretectal area for the light reflex, nevertheless the macula is very well represented on the superior colliculus in the pigeon as well as the area centralis in the rabbit and goat. In this respect the

rabbit is included whether it has a real macula or not, but the important thing is the presence of an area for detailed central vision. In fact it was found that macular area is the one relatively occupying the bigger portion of the colliculus compared with the peripheral retina, and even this enormous representation is not proportionate because in the rabbit, the horizontal plane was found much better represented than the vertical one. This is also true for the goat although in addition the lower field is slightly more represented than the upper. In the pigeon it is the lower part of the central field which has enormous representation. It seems probable that these differences are related to the position of the head of the animal in normal life. The rabbit with its head very near to the ground would need more detailed information about the world in front of and behind it than down. Again the goat with its long neck and high head and the pigeon when flying high, both need a well represented lower visual field.

Freeman and Papez (1930) and Layman (1936) proved that rats with lesions in the superior colliculus could learn a brightness discrimination in the normal learning time and Layman (1936) found that rats with lesions in the superior colliculus alone could learn to discriminate striations as well as normal animals. These

workers had shown that the superior colliculus is not essential for brightness discrimination nor for pattern vision. Although the superior colliculus may play a part in these functions as suggested by Ghiselli (1937), because they do not disappear when the cortex is removed (with subsequent retrograde degeneration of the lateral geniculate body which is the other subcortical visual centre) yet it is not its main function, nor is it the site for the long disputed light reflex.

The results of this study show how minutely the retina is represented on the superior colliculus in two mammals and a bird. Added to this, the connections of the superior colliculus from the retina and occipital cortex on the one hand and to the oculomotor nuclei, cranial nerve nuclei and neck muscles centres in the spinal cord on the other hand, there is no doubt that this centre has some important function as regards eye movements.

Because of the small size of the superior colliculus in monkey and man, and since Brouwer and Zeeman failed to obtain a convincing projection of the retina on the superior colliculus in monkey, it has frequently been stated that in monkey and man the superior colliculus receives an insignificant number of optic fibres, and hence the unimportance of this structure in higher mammals emphasized. This conception is extremely erroneous. The crude method Brouwer and Zeeman used to trace optic fibres going to the midbrain region is not at all a

proof that the retina is not well projected on the superior colliculus, since it is well known that these fibres are lightly myelinated. It is true that the colliculus of animals like the rat, rabbit, goat and birds is enormous, but again the colliculus of the cat is also small or even much smaller compared with that of monkey and man, and yet when Apter used electrical methods, she obtained the most detailed representation of the retina on the surface of the superior colliculus. The statement that in man the superior colliculus receives an insignificant number of fibres from the retina is not based on any direct observation.

It is well known that stimulation of the colliculus leads to conjugate deviation of the eyes to a certain point in the field depending on the point of the colliculus stimulated. Hess, Büngi and Bucher (1945) demonstrated that stimulation of the superior colliculus led to co-ordinate movements of the eyes and head towards the opposite side, the direction depending on the part stimulated. Hess interprets the tectal reaction as a "visual grasp reflex".

The results of Hess et al are not so clear as Apter's who used the strychninemethod and gave a very detailed map. It seems probable that in such experiments using stimulation to a small area as the superior colliculus one should be very

careful (as Apter did) and so avoided a strong stimulus which is certainly liable to spread more than is intended. The results of Hess et al should be accepted in a broad sense i.e. in a sense that there is localization on the superior colliculus as regards direction of gaze, whereas Apter's map should be considered the real localization of ocular movements. Goldman (1947) observed a kind of subcortical reflex movement in man involving almost exclusively the eyes.

The results of Apter's work by applying strychnine to the surface of the colliculus and flashing light to the whole eye, when the gaze is directed into certain direction, also the paralysis of gaze in patients with pineal body tumour and how it proceeds in accordance with the chart of mapping obtained by Apter were referred to.

Most authors agree that the superior colliculus in mammals at least is connected to the oculomotor nuclei in a definite manner. (Kappers, Huber and Crosby 1939) Now that more is known about the role of the superior colliculus in eye movements in the light of the work of Apter and Hess it seems to be necessary to revise the question of the projection of superior colliculus on the oculomotor complex.

There is no doubt that the cortico mesencephalic fibres end in the superior colliculus but whether the fronto-mesencephalic fibres go directly to the oculomotor nuclei or first relay in

the superior colliculus is disputed. Anyhow in the monkey at least it was shown by Crosby et al (1948) that they pass directly to the oculomotor nuclei without establishing any connections with the superior colliculus.

Boyce (1895) working on the cat suggested that fronto-mesencephalic fibres end in the superior colliculus and Simpson (1901) found the same in cat, but not in dog nor monkey.

Recently Henderson and Crosby (1952) found that the occipito mesencephalic fibres arise in the cortex rostral to area 19, but these authors were not sure in the material available to them whether they arise from area 17 or area 18. Fibres arising from the upper part of this occipital region have been traced to the caudolateral end of the superior colliculus, and these from the lower portion of this occipital area to the fronto-medial portion of the tectal region.

It seems from the results of Crosby et al referred to above that the frontal cortex does not act on the superior colliculus. This means that the superior colliculus is not a centre of the voluntary eye movements initiated in the frontal eye field (8 and 6). From the established relation of the occipital eye field, one concludes that the superior colliculus is involved in the involuntary eye movements (fixation reflex).

The connections of the superior colliculus with cranial nerve nuclei and centres of neck muscles in the cervical portion of the spinal cord via the tecto spinal tract are of extreme importance. Involuntary or voluntary movements of the head and neck towards an object in the field of vision is mediated through this tract. In man the extra ocular eye muscles are much more functioning than in lower mammals where the head and neck muscles play a more important part in the direction of gaze than in man. This is why the tecto spinal tract is not well developed in man compared with an animal like the cat.

Added to this the connection of the superior colliculus to the inferior colliculus which makes the direction of gaze to a sound stimulus possible, shows how the superior colliculus is establishing so varied andimportant connections with afferent paths on the one hand and the efferent systems concerned with movements of eyes head and neck on the other hand. This relationship is remarkably well mapped everywhere in the visual pathway: retina minutely projected on superior colliculus, occipital cortex (being a cerebral retina itself) also well projected on the same lower centre, and this in turn projected to the oculomotor complex in such a definite manner that if one part of the colliculus is stimulated by a

visual stimulus in the field, then this part of the colliculus, being connected to the part of the oculomotor complex that would direct the eyes towards that point in the field would thus complete the visual reflex arc.

The argument that the superior colliculus has some importance in vision in lower mammals as evidenced by the retention of conditional response which has been established on light stimulus after the extirpation of the occipital cortex does not mean anything. All animals investigated (rat, dog, monkey) are known to have a visual cortex and the argument that in man, on the other hand there is complete blindness after lesions involving the occipital pole does not mean that lower animals depend on the superior colliculus for vision. The only possibility is that with the process of corticalization of function, it happened that the visual cortex in monkey and more in man has assumed more functional importance and that the influence it exercises on the superior colliculus (as a lower visual centre) is more pronounced.

SUMMARY

1. A historical review of the available literature is given about the structure of the superior colliculus and its connections with the cerebral cortex, inferior colliculus, oculomotor nuclei, cranial nerve nuclei and the centres for neck muscles in the cervical portion of the spinal cord, together with the projection of retina on the surface of the superior colliculus. Also the role of the superior colliculus in eye movements, brightness discrimination and pattern vision.

2. The methods of investigation in this study depend on using the stereotaxic head holder and a micrometer scale to insert microneedle electrodes into the various layers of the superior colliculus of rabbit and goat and the optic tectum of the pigeon. These structures were then cut serially in celloidin sections and the needle tracks were identified. An interrupted neon light of 1mm diameter was used as stimulus and mounted on a perimeter.

3. The results showed a point to point representation of the retina on the superior colliculus in each of the three animals, and in the deeper layers in the rabbit and goat certain patterns were obtained from the field of vision. These patterns were either radiating from the fixation point or concentric with it.

4. The electrical responses obtained were of two components in the three animals, one with short latency and well localized and the other with long latency and more or less diffuse. The origin of each is explained.

5. The histological results confirmed the existence of the stratum zonale and the presence of large cells in the stratum opticum is emphasized.

6. The role of the superior colliculus as a centre for involuntary eye movements is discussed and a suggestion of the importance of the patterns obtained from the deeper layers is explained according to Pitts and McCullochs theory about the presence of two co-ordinates in the superior colliculus.

7. The connections of the tectospinal tract is referred to and its importance in movements of the eyes and head especially in lower animals.

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